MARSUPIAL FROGS

Gastrotheca & Allied Genera

William E. Duellman

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Marsupial Frogs

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William E. Duellman

With Osteology by Linda Trueb

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To Linda

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Preface

ONE NIGHT IN JULY 1963, WHILE COLLECTING IN PRISTINE RAINFOREST AT Laguna in the Serranía de Darién, Panama, the light from a headlamp caught the reflection of the eyes of a large frog; moments later a female marsupial frog, *Gastrotheca cornuta*, with eggs in her brood pouch, was captured. At the same locality Charles W. Myers and I were frustrated by not being able to locate the sources of loud "bops" coming from the trees. Two years later, near Almirante at the other end of Panama, the evasive "tree-top bopper" was identified as the same species of marsupial frog. During the course of my early fieldwork in the Andes of Ecuador in 1967 and 1968, I collected several specimens of a much smaller marsupial frog then referred to the taxon *Gastrotheca marsupiata*. The differences in size, appearance, and reproduction (production of tadpoles versus direct development) fascinated me. My former mentor, the late Charles F. Walker, had an intense interest in these marsupial frogs; he shared his knowledge of them with me and encouraged me to investigate their taxonomy and evolution.

Thus began five decades of research on the egg-brooding marsupial frogs and their allies. When I began this investigation, the available specimens in museums were woefully inadequate to answer the questions being asked. Therefore I spent more than two-and-a-half years in the field—from the Guiana Highlands of Venezuela to the Andes of Argentina—in an effort to gather more specimens and new kinds of data. Sometimes the results of the fieldwork seemed to raise more questions than they answered; often, instead of finding species for which I was searching, I discovered previously unknown species. I was able to gain field experience with many of the species and learn much about the biology of many of them. My investigations of these frogs seem to have taken an inordinate amount of time. It soon became obvious that the taxonomy of the group was chaotic and that classical taxonomic procedures were not going to resolve the problems. Some of the techniques I wanted to apply to marsupial frogs were beyond my expertise, so I enlisted the cooperation of a variety of colleagues. Thus, in the ensuing years, investigations were completed on the embryology, karyology, allozymes, serum albumins, DNA, and osteology of the egg-brooding frogs.

The principal goal of this research has been the interpretation of the evolution of egg brooding and direct development in the marsupial frogs and their allies. In order to accomplish this goal, it is necessary to have a sound taxonomy of the species and testable hypotheses of phylogenetic relationships upon which to superimpose the features of reproductive biology. Thus diverse endeavors over the past five decades have greatly enhanced our knowledge of the marsupial frogs and their allies. Many questions remain to be answered. While I and others continue our efforts, I contribute this work to the memory of the late Charles F. Walker, a true gentleman and scholar, to whom marsupial frogs were something special.

Acknowledgments

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For providing me with field data, recordings of calls, and/or photographs of living specimens, I am deeply grateful to Aldemar Acevedo, Juan C. Arredondo, César L. Barrio-Amorós, the late Werner C. A. Bokermann, Alessando Catenazzi, Germán Chávez, Luis A. Coloma R., Ignacio De la Riva, Manuella Folly, Mauricio Forlani, the late Eugenio Izecksohn, Célio F. B. Haddad, Karl-Heinz Jungfer, Jörn Köhler, Philippe J. R. Kok, William W. Lamar, the late Raymond F. Laurent, Edgar Lehr, John D. Lynch, Roy W. McDiarmid, the late Scott J. Maness, Charles W. Myers, Ivan Nunes, José Ernesto Pérez Villota, José Pombal Jr., Fernando J. M. Rojas-Runjaic, the late Pedro M. Ruíz-C., Marco A. Serna, Mauro Teixeira Jr., Vivian Trevine, Marcos Vaira, Pablo Venegas, Ciao Vinicius de Mira Mendes, and Mario H. Yanez-Muñoz.

The majority of the specimens and associated field data were collected by me and my field companions. Marsupial frogs were encoun-

tered first in Panama during the 1960s, when I was fortunate to be able to visit many areas of virgin cloud forest, accompanied by Charles W. Myers and Linda Trueb. My first intensive fieldwork on marsupial frogs was accomplished in Peru with Thomas H. Fritts, the late Ismael Ceballos B., and Oscar Ochoa in 1971. Later that year and in 1972, I made two trips to Ecuador for the expressed purpose of obtaining more material on marsupial frogs. During those trips I was accompanied at various times by Joseph T. Collins, Bruce MacBryde, John E. Simmons, and Linda Trueb. Much material was obtained during a 15-month trip through the length of the Andes in 1974–1975, during which time Dana Trueb Duellman, John E. Simmons, and Linda Trueb worked diligently to enhance the collections, which were augmented by short visits by Juan R. León and Alan H. Savitzky. In 1977 David C. Cannatella joined me in the field in southern Peru, and in 1979 he and Thomas J. Berger shared with me some miserable accommodations in northern and central Peru. Also in 1979, I ascended the slopes of Cerro Tamá on the Colombian-Venezuelan border; the success of that trip was due to the efforts of Amelia Díaz de Pascual and Jaime E. Péfaur. Fieldwork in Colombia in 1979 was successful, thanks to the enthusiastic assistance of Fernando Castro H. A collection of marsupial frogs was made in central Peru in 1983, with the aid of B. Anthony Luscombe and Patsy and the late Clarence J. McCoy. Collections were made in Ecuador in 1984, with the determined assistance of Patricia A. Burrowes, David M. Hillis, and John E. Simmons. Finally, my field studies were completed in Peru in 1989, where I was assisted by Fernando M. Cuadros, Michael E. Morrison, and John J. Wiens. I am indebted to all of them for their significant contributions, often made under extremely adverse conditions. Although we never worked in the field together in South America, John D. Lynch added to my database considerably through his fieldwork in Colombia and Ecuador.

I never worked in the field in eastern Brazil, where a cadre of interesting marsupial frogs live. I gathered insights second hand from a host of Brazilians, including Hélio R. da Silva, Célio F. B. Haddad, Eugenio Izecksohn, Ivan Nunes, José Pombal Jr., Sergio Potsch de Carvalho-e-Silva, Mauro Teixeira Jr., Miguel Trefaut Rodrigues, Marina Walker, and Hussam Zaher. They deserve my profound thanks.

For their logistical support in the field, I am indebted to the late Raymond F. Laurent in Argentina, Stephen C. Ayala and Antonio d'Lessandro in Colombia, Ing. Miguel Moreno Espinoza and Eugenia del Pino in Ecuador, B. Anthony Luscombe in Peru, and Jaime E. Péfaur in Venezuela. Permits for the collection and exportation of specimens were issued in Colombia by the late Jorge Hernández-C. of INDERENA; in Ecuador by Sergio Figueroa of the Programa Nacional Forestal, Ministerio de Agricultura; and in Peru by Luis J. Cueto Aragón, Armando Pimental Bustamente, and José Purisaca of the Dirección Forestal y de Fauna, Ministerio de Agricultura.

Several colleagues who have worked in South America have provided material that has been incorporated herein; thus I thank César Aguilar, Alessandro Catenazzi, Ignacio De La Riva, Jörn Köhler, Edgar Lehr, Daniel Rodríguez, Mauro Teixeira Jr., Pablo J. Venegas, and Rudolf von May.

During the five decades that I actively worked on marsupial frogs in the laboratory, I benefited from the dedicated assistance of several graduate students. First and foremost, I am greatly indebted to Rebecca A. Pyles, who measured the frogs, recorded my observations on external structure and coloration, managed the data files, and completed the univariate and multivariate data analyses. Rafael de Sá skillfully prepared dry skeletons and cleared and stained specimens, and he also assisted with the audiospectrograms. Peter Gray counted and measured eggs and Thomas J. Berger recorded data on tadpoles. Charles W. Linkem greatly aided in the preparation of this monograph by creating distribution maps and providing statistical analyses. Finally, DNA sequencing and phylogenetic analyses were performed by Anthony J. Barley, who helped immensely in putting the finishing touches on this volume.

The multidisciplinary approach to the systematics and evolution of marsupial frogs was possible only through collaboration with other investigators: James P. Bogart and Michael Schmid, karyology; David M. Hillis, allozyme electrophoresis; Linda R. Maxson, microcomplement fixation of serum albumins; Linda Trueb, osteology; Richard J. Wassersug, larval buccal morphology; and Anthony Barley, David C. Blackburn, S. Blair Hedges, and John J. Wiens, DNA analyses.

The illustrations in this book are the results of the talents of Gretchen Bracher, Linda S. Dryden, Amy Lathrop, Anne A. Musser, Jennifer B. Pramuk, and Linda Trueb; I thank them for their fine drawings that enhance this publication. Also, I am indebted to Andrew Campbell, Mauricio Forlani, and Ivan Nunes for photographs of preserved specimens. This monograph is enriched by many color photographs of living hemiphractid frogs. Approximately half of those photographs were taken by me; the other half were taken by numerous individuals. I am indebted to Werner C. A. Bokermann, Patricia A. Burrowes, Alessandro Catenazzi, Germán Chávez, Luis A. Coloma, Ignacio De la Riva, Iuri Ribeiro Dias, Thomas H. Fritts, Célio F. B. Haddad, Caio Vinicius de Mira Mendes, Ivan Nunes, the late Eugenio Izecksohn, Jörn Köhler, Philippe J. R. Kok, William W. Lamar, Raymond F. Laurent, Edgar Lehr, Cyro de Luna-Dias Neto, John D. Lynch, Roy W. McDiarmid, Charles W. Myers, Bruno Pimenta, H. Plenge, José P. Pombal Jr., Pedro M. Ruíz-C., Mauro Teixeira Jr., Vivian Trevine, Marcos Vaira, and Pablo Venegas.

I am especially indebted to Linda Trueb, who not only accompanied me in the field on many occasions and provided the osteological data and drawings incorporated herein, but also critically read much of the text and provided a sounding board for the evolution of my ideas for more than five decades of work on marsupial frogs.

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Marsupial Frogs

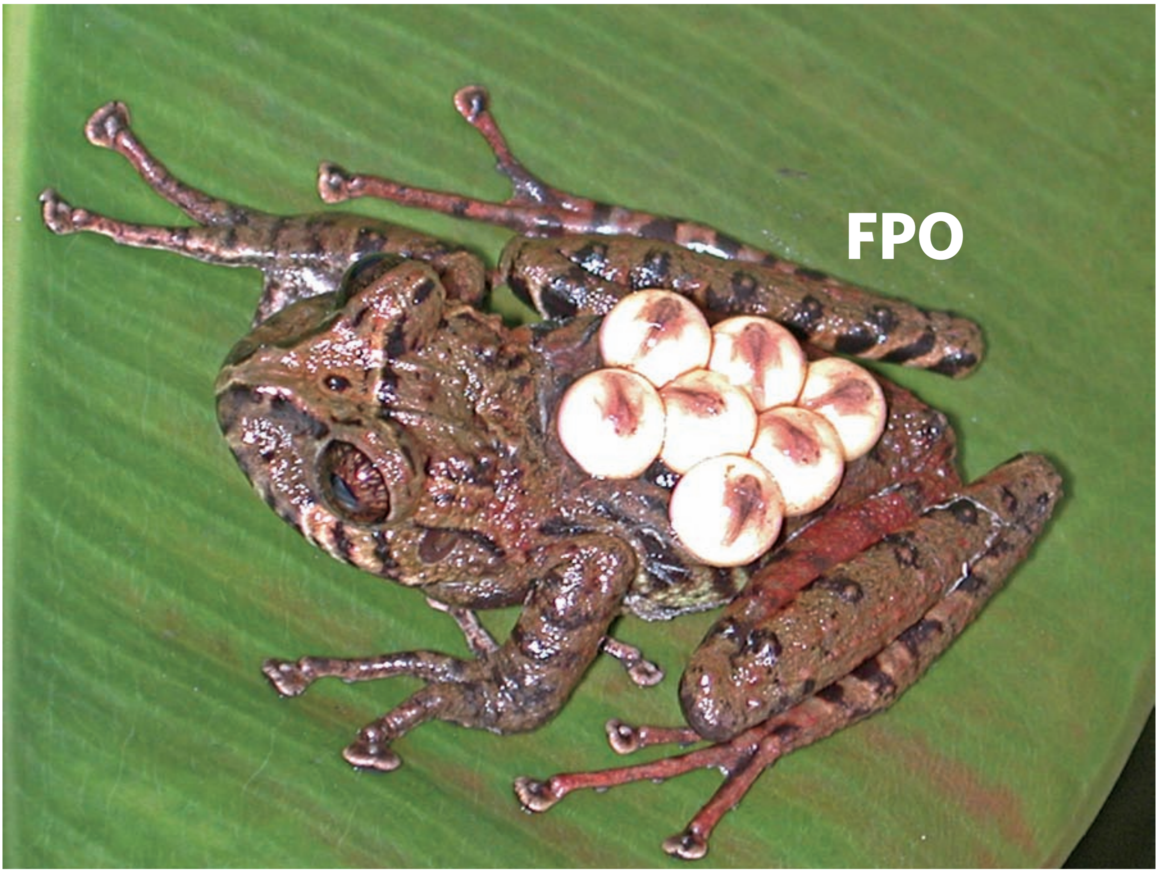

Fig. 1.1 Brooding female *Stefania ayangannae* (KU 315003), Mt. Kopinang, Guyana. Note the tadpole-like embryos with external gills. Photo by D. B. Means, KUDA.

1

Introduction

What are marsupial frogs, and why are they so particularly worthy of study? These are the only frogs in which males fertilize the eggs out of the water and then place them in a pouch on the back of the female. The developing embryos of marsupial frogs and their allies—i.e., the amphibian family Hemiphractidae—have large external bell-shaped or sheet-like gills that are unlike those of any other lineage of frogs. These behavioral and developmental features are unique to marsupial frogs and their allies.

Many lineages of anurans have circumvented the generalized mode of life history incorporating free-living aquatic larvae, and in a number of these lineages the eggs develop directly into froglets. Some hemiphractids (*Flectonotus* and *Fritziana*) produce free-living non-feeding tadpoles, whereas others (*Cryptobatrachus*, *Hemiphractus*, and *Stefania*) produce froglets (Fig. 1.1). The marsupial frogs of the genus *Gastrotheca* are unusual, because some species produce free-living feeding tadpoles, whereas others produce froglets. Thus it is understandable that these frogs are intrinsically of interest to developmental biologists and those persons concerned with the evolution of life histories.

Considerable effort has been directed at systematic studies of hemiphractid frogs. Trueb (1974) reviewed the bizarre genus *Hemiphractus*. *Flectonotus* and *Fritziana* were revised by Duellman and Gray (1983) and by Duellman et al. (2011b), and *Fritziana* has been studied most recently by Folly et al. (2014). The systematics of *Stefania* was treated by Duellman and Hoogmoed (1984) and subsequently by Señaris et al. (1997) and MacCulloch and Lathrop (2002). The late Pedro M. Ruíz-C. left an unfinished manuscript on the systematics of *Cryptobatrachus*; this was later revised and published by Lynch (2008).

The taxonomy of *Gastrotheca* has been extraordinarily difficult. Numerous papers have dealt with the *Gastrotheca* of different regions, and several have included descriptions of new taxa: Duellman and Fritts, 1972; Duellman, 1974, 1977, 1980, 1983a, 1983b, 1984, 1987a, 1987b, 2013; Trueb and Duellman, 1978; Duellman and Pyles, 1980; Duellman and Burrowes, 1986; Duellman and Hillis, 1987; Duellman and Trueb, 1988; Duellman et al. 2001, 2004; Duellman and Köhler, 2005; Duellman and

Venegas, 2005; and Duellman et al. 2006, 2011a, 2014. Other published studies have dealt with certain aspects of the systematics and evolution of the egg-brooding hylids: serum albumins (Scanlan et al., 1980; Duellman et al., 1988), molecular phylogeny (Wiens et al., 2007; Heinicke et al., 2009; Blackburn and Duellman, 2013), pouch morphology (del Pino, 1980), developmental biology (del Pino et al., 1975; del Pino and Escobar, 1981; del Pino and Elinson, 1983), reproduction (Duellman and Maness, 1980), ontogenetic polychromatism (Duellman and Ruíz-Carranza, 1986), oral structures of larvae and embryos (Wassersug and Duellman, 1984), myology (Tyler and Duellman, 1995), and karyology (Schmid et al., 1988, 1990, 2012). Moreover, Brazilian biologists have recently expanded our knowledge of the species in eastern Brazil (e.g., Caramaschi and Rodrigues, 2007; Izecksohn and Carvalho-e-Silva, 2008; Teixeira et al., 2012).

The present work is an interpretation of the phylogenetic relationships among the species of *Gastrotheca* and among the genera of Hemiphractidae. The history of the nomenclature and classification of hemiphractid frogs is presented in chapter 2. Phylogenetic relationships and a classification based on them are treated in chapter 3. Chapter 4 contains a detailed account of cranial osteology written and illustrated by Linda Trueb, and chapter 5 deals with external morphological characters. Other features used in the systematics of hemiphractid frogs are discussed in chapter 6. The evolution of specialized reproductive modes is treated in chapter 7. In chapter 8 the postulated evolutionary history of the frogs is examined with respect to the appropriate historical geology and paleoclimatology of South and Central America.

The classification of hemiphractid frogs presented in this book is based on a reconstruction of their phylogenetic relationships. In chapter 9, each genus is diagnosed, the content and distribution of each is determined, and intrageneric relationships are discussed. In chapters 10–12, I provide a complete taxonomic review of the genus *Gastrotheca*, in which defined clades are recognized as subgenera. I have also included all available data on this genus. The descriptions can include information on subadults and juveniles, whereas the tables generally contain data on adults only. Also, some tables incorporate measurements that were not available when the descriptions were written. To someone not familiar with these frogs and the difficulties associated with their taxonomy, it may seem that I have supplied too much detail in the diagnoses and descriptions. The data are presented in a standardized manner that should facilitate studies by future workers. I have no illusions that this volume is the last word on marsupial frogs of the genus *Gastrotheca*. Additional species certainly will be found in the future, and quite likely some of the species that I recognize are composites.

Materials and Methods

During the course of this study I have examined 4661 preserved adults and subadults, 191 lots of tadpoles, 264 young, 95 dried skeletons, 66 cleared-and-stained specimens (external data were recorded on many specimens prior to their being prepared as skeletons), and 9 sets of eggs and embryos (exclusive of those in the pouches of preserved specimens). Material used in this study is housed in 78 collections on three continents; the numbers of different kinds of preparations for each species are listed in appendix 1 in the supplemental material (www.press.jhu.edu). The specimens and their localities are listed in appendix 2 in the supplemental material. All specimens are referred to by their catalogue numbers, preceded by an abbreviation.

AL-MN	Adolpho Lutz Collection (deposited in MNRJ), Brazil
AMNH	American Museum of Natural History, New York, USA
ANSP	Academy of Natural Sciences of Philadelphia, USA
BMNH	British Museum (Natural History), London, UK
BYU	Brigham Young University, Provo, US
CAS	California Academy of Sciences, San Francisco, USA
CAS-SU	Stanford University Collection (now in CAS), San Francisco, USA
CBF	Colección Boliviana de Fauna, La Paz, Bolivia
CET	Centro de Estudios Tropicales, Sevilla, Spain
CFBH	Célio Haddad Collection (deposited in the Universidade Estadual Paulista), Rio Claro, Brazil
CGB	Centro de Biodiversidad y Genética, Universidad Mayor de San Simón, Cochabamba, Bolivia
CHUFRPE	Coleção Herpetólogica da Universidade Federal Rural de Pernambuco, Recife, Brazil
CJ	Centro Jambatu, Quito, Ecuador
CM	Carnegie Museum, Pittsburgh, USA
CORBIDI	Centro de Ornitología y Biodiversidad, Lima, Peru
CSJ	Colegio San José, Medellín, Colombia
CVULA	Colección de Vertebrados, Universidad de Los Andes, Mérida, Venezuela
DFCH-USFQ	Universidad San Francisco, Quito, Ecuador
EBRG	Estación Biológica Rancho Grande, Maracay, Venezuela
EDP	Eugenia del Pino Collection, Pontífica Universidad Católica del Perú, Quito, Ecuador
EI	Eugenio Izechsohn Collection, Rio de Janeiro, Brazil
EPN	Escuela Politécnica Nacional, Quito, Ecuador
FML	Fundación Miguel Lillo, Tucumán, Argentina
FMNH	Field Museum of Natural History, Chicago, USA
FSM	Florida State Museum, Gainesville, USA
ICN	Instituto de Ciencias Naturales, Museo de Historia Natural, Bogotá, Colombia
INDERENA	Instituto Nacional para la Conservación de Recursos Naturales, Bogotá, Colombia
KU	Biodiversity Institute, University of Kansas, Lawrence, USA
LACM	Los Angeles County Museum, Los Angeles, USA
LSUMZ	Louisiana State University Museum of Zoology, Baton Rouge, USA
MBML	Museu de Biologia Prof. Mello Leitão, Santa Teresa, Espírito Santo, Brazil
MBUCV	Museo de Biología, Universidad Centroccidental, Barquisimeto, Venezuela
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, USA

MECN	Museo Ecuatoriana de Ciencias Naturales, Quito, Ecuador
MHNC	Museo de Historia Natural, Universidad San Antonio del Abad, Cusco, Peru
MHNG	Musée d'Histoire Naturelle, Geneva, Switzerland
MHNLS	Museo de Historia Natural La Salle, Caracas, Venezuela
MIZA	Museo del Instituto de Zoología Agrícola de la Universidad Central de Venezuela, Maracay, Venezuela
MLS	Museo del Instituto de La Salle, Bogotá, Colombia
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MNK	Museo de Historia Natural "Noel Kempff Mercado," Santa Cruz de la Sierra, Bolivia
MNRJ	Museu National, Rio de Janeiro, Brazil
MTD	Museum für Tierkunde, Dresden, Germany
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley, USA
MZUBFA	Museu de Zoologia da Universidade Federal da Bahia, Salvador, Brazil
MZUEFS	Museu de Zoologia, Universidade Estadual de Feira de Santana, Feira de Santana, Brazil
MZUESC	Museu de Zoologia Universidade Estadual de Santa Cruz, Ilhéus, Brazil
MZUF	Museo Zoologico de la Specola, Universita di Firenzi, Florence, Italy
MZUFV	Museu de Zoologia Universidade Estadual de Visçoa, Visçoa, Brazil
NHMG	Naturhistoriska Museet, Göteborg, Sweden
NHRM	Naturhistoriska Riksmuseet, Stockholm, Sweden
NMW	Naturhistorisches Museum, Vienna, Austria
QCAZ	Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador
RMNH	Nationaal Natuurhistorisch Museum, Leiden, Netherlands
RNLP	Reserva Natural La Planada, Ricuarte, Colombia
RURAL	Departamento de Biologia Animal, Universidad Federal Rural do Rio de Janeiro, Seropédica, Brazil
SMF	Naturmuseum und Forschungsinstitut, Senckenberg, Germany
TNHC	Texas Natural History Collection, Texas Memorial Museum, Austin, USA
UCR	Universidad de Costa Rica, San José, Costa Rica
UFAL	Universidade Federal de Alagoas, Maceló, Brazil
UIMNH	University of Illinois, Museum of Natural History, Urbana, USA
ULALB	Universidad de Los Andes, Laboratorio de Biogeografía, Mérida, Venezuela
UMMZ	University of Michigan, Museum of Zoology, Ann Arbor, USA

UNSSA	Universidad Nacional San Antonio de Abad, Cusco, Peru
USNM	National Museum of Natural History, Washington, USA
UTA	University of Texas, Arlington, USA
UV	Universidad del Valle, Cali, Colombia
WCAB	Werner C. A. Bokermann Collection (deposited in Museu de Zoologia, Universidade de São Paulo), Brazil
WWL	William W. Lamar Collection, Tyler, Texas, USA
ZFMK	Zoologisches Forschunginstitut und Museum Alexander Koenig, Bonn, Germany
ZMB	Universität Humboldt, Museum für Naturkunde, Berlin, Germany
ZMJU	Zoological Museum, Institute of Zoology, Jagiellonian University, Kraków, Poland
ZMUC	Københavens Universitët Zoologisk Museum, Copenhagen, Denmark
ZSM	Zoologisches Sammlung des Bayerischen Staats, Munich, Germany
ZUEC	Museu de História Natural, Universidade Estadual de Campinas, Brazil
ZUFRJ	Departamento de Zoologia, Insituto de Biología, Universidad Federal do Rio de Janeiro, Brazil.

Adult frogs preserved in 70% ethanol were used for measurements and external characters; these are discussed in detail in chapter 5, where characteristics of tadpoles also are defined. Osteological data were obtained from the examination of dry skeletons and alizarin-alcian-stained specimens (Dingerkus and Uhler, 1977); these are treated in detail in chapter 4. The terminology of cranial characters follows Trueb (1993), and that of postcranial osteological characters, Duellman and Trueb (1986); the methods of measuring elements and angles follow Trueb (1977).

Eggs and Development

Most of the data on clutch and egg sizes were obtained from an examination of eggs taken from the pouches of brooding females. After the eggs were counted, the diameters of 10 eggs were measured to the nearest 0.1 mm, using needle-nosed dial calipers. Developing embryos were staged by Gosner's (1960) method. The volumes of the eggs were calculated by considering the eggs to be spherical, which is the case for eggs in the early stages of development. The total clutch volume was calculated by multiplying the number of eggs by the mean volume of an egg.

Ovarian eggs were considered to be mature if they approximated the size of the eggs in brooding females of the same species. Counts of ovarian eggs were compared with the numbers of eggs in the pouches. In those few instances when the type of development was not known, it was hypothesized on the basis of the sizes of eggs of the species of unknown mode with those of a species of known mode.

Three reproductive modes usually are recognized in marsupial frogs: (1) eggs hatching as tadpoles that complete their development as free-living feeding larvae (some *Gastrotheca*); (2) eggs hatching as advanced tadpoles, with fully formed limbs, that complete their development as free-living non-feeding larvae (*Flectonotus* and *Fritziana*); and (3) eggs hatching as froglets, without a free-living larval stage (*Cryptobatrachus*, *Hemiphractus*, *Stefania*, and some *Gastrotheca*). In *Gastrotheca* that produce tadpoles, the tadpoles hatch at a relatively advanced stage. Thus four categories are recognized: (1) early-stage feeding tadpoles; (2) late-stage feeding tadpoles; (3) late-stage non-feeding tadpoles; and (4) froglets.

Advertisement Calls

For those species for which analyzable tape recordings are available, the following terminology is used.

Call. The entire assemblage of signals is produced in a given sequence. In some species the call consists of a single note, whereas in others it consists of two or more notes.

Call rate. The rate at which calls are produced is measured in calls per minute. In those species that call infrequently, as is the case in most *Gastrotheca*, the temporal component is given as the interval in minutes between calls.

Primary note. In several species of *Gastrotheca* that have a multinote call, the first note is longer and more emphasized than the succeeding notes. This primary note may be produced alone or followed by other notes.

Secondary notes. Secondary notes are those the primary note. Occasionally they are produced without a primary note.

Note-repetition rate. The rate in time in which notes are produced in a multinote call, expressed in notes per minute.

Pulse rate. The pulsations on the temporal scale are counted per note and expressed as pulses per second.

Fundamental frequency. The term refers to the lowest-pitched harmonic. In many audiospectrograms of *Gastrotheca* the lower frequencies are masked by poor modulation, so it is not possible to determine the fundamental frequency, which is expressed in hertz.

Dominant frequency. This harmonic is resonated with greater emphasis than other harmonics and is expressed in hertz.

Karyology

Tissues for an examination of chromosomes were prepared in the field. Living frogs were injected with 0.1% solution of colchicene in distilled water; 8–10 hours later the intestine was removed, washed in distilled water, and preserved in a solution of 3 parts 100% ethanol and 1 part glacial acetic acid. Subsequently these tissues were analyzed by Michael Schmid, whose research on hemiphractid frogs resulted in an intensive study of many taxa (Schmid et al., 2012).

Biochemical Analyses

Prior to the genomic studies, some phylogenetic analyses were based on allozymes and serum albumins.

Allozymes

Tissues for electrophoretic studies were available from a limited number of species from the Andes of Colombia, Ecuador, and Peru. All electrophoretic work was performed by David M. Hillis. The electrophoretic comparison of tissues obtained from tadpoles and adults from the same population revealed no differences. In the field, liver and muscle tissues were removed from the frogs and immediately placed in liquid nitrogen for transport to the laboratory, where they were maintained at 0°C. Tissues were ground with a teflon homogenizer and diluted 1:1 (muscle) or 1:3 (liver) with 0.01 M tris - 0.001 M EDTA - 0.001 M ß-mercaptoethanol, pH 7.5. Homogenates were centrifuged at 15,000 rpm for 5 minutes; supernatants were refrozen at −80°C prior to use. The procedures for horizontal starch gel electrophoresis followed Selander et al. (1971), as modified by Duellman and Hillis (1987). The staining procedures followed Selander et al. (1971), Harris and Hopkinson (1976), and Siciliano and Shaw (1976). The phosphorescent stains (acid phosphatase, β-glucuronidase, and α-mannosidase) were viewed and photographed under 375 mm UV light.

Serum Albumins

Plasma and/or muscle tissue was removed in the field and preserved in phenoxyethanol. All analyses were accomplished at the University of Illinois and the Pennsylvania State University by Linda R. Maxson and her associates. The albumin antisera were prepared according to established procedures (L. Maxson et al., 1979). All antisera were used in the quantitative microcomplement fixation (MC′F) assay (Champion et al., 1974; R. Maxson and Maxson, 1986) to estimate albumin evolution. Data are reported as immunological distances (ID). For albumin, it has been determined that one unit of ID is approximately equivalent to one amino acid difference between the albumins that are compared (L. Maxson and Wilson, 1975; R. Maxson and L. Maxson, 1986) and that approximately 10 such substitutions accumulate every 5.5–6.0 million years of separation of lineages (Wilson et al., 1977).

Genomic Studies

Tissues collected in the field in the 1970s were preserved in phenoxyethanol; those collected from the mid-1980s onward were preserved in liquid nitrogen or in 95% ethanol. For the molecular analyses, two mitochondrial genes (16S ribosomal RNA; NADH dehydrogenase subunit 1, or ND1) and two nuclear genes (recombination activating gene 1, or RAG-1; proopiomelanocortin, or POMC) were targeted for sequencing. In all cases, the same primers were utilized for polymerase chain reaction (PCR) amplification and sequencing. For 16S, the primers 16Sc and 16Sd (Darst & Cannatella, 2004) were used; for ND1, HEMI1-F and HEMI1-R (Wiens et al., 2007); for RAG-1, RAG1-Hemi-f2 and RAG1-Hemi-r2 (Blackburn and Duellman, 2013); and for POMC, POMC-1 (Wiens et al.,

2007) and POMC-Hemi-f (Blackburn and Duellman, 2013). Voucher specimens and their sequences are tabulated in appendix 3 in the supplemental material (www.press.jhu.edu).

Genomic DNA was extracted from soft tissue utilizing a guanidine thiocyanate protocol (Esselstyn et al., 2008). DNA was amplified using standard PCR protocols, as outlined in the original publications where the primers were used. The products were purified with a 20% dilution of ExoSAP-IT (US78201, Amersham Biosciences, Piscataway, NJ), incubated for 30 minutes at 37°C, and then at 80°C for 15 minutes. The cleaned PCR products were dye labeled using Big-Dye terminator 3.1 (Applied Biosystems, Foster City, CA), purified using Sephadex (NC9406038, Amersham Biosciences, Piscataway, NJ), and sequenced on an ABI 3730 automated capillary sequencer. All PCR products were sequenced in both directions.

The sequences were edited and subsequently aligned using MAFFT in Geneious Pro, version 5.3 (Katoh et al., 2005). The alignments were visually examined, translated, and adjusted if necessary using MacClade, version 4.07 (Maddison and Maddison, 2003). The models of molecular evolution were selected using decision theory implemented in DT-Modsel (Minin et al., 2003). In all cases, the most complex model of nucleotide evolution was chosen, GTR + Γ. The phylogenetic analyses were conducted in both maximum likelihood and Bayesian frameworks. In both cases, the data were concatenated and partitioned by gene for analysis. The maximum likelihood phylogenetic analysis was performed using RAxML, version 7.03 (Stamaktakis, 2006), with support being assessed via 1000 bootstrap replicates; the tree was rooted with *Eleutherodactylus curtipes*.

In order to obtain an estimate of the timeframe for diversification within *Gastrotheca*, divergence time estimation was performed using two different calibration strategies in BEAST, version 1.7.5 (Drummond & Rambaut, 2007). In the first strategy, the phylogeny was calibrated by applying a 1.91% substitution rate per million years for the ND1 data (Crawford, 2003; Wang et al., 2008). In the second strategy, a calibration point was assigned to the node demarcating the divergence between hemiphractids and terraranas, as estimated by Heinicke et al. (2009). A normal distribution prior was placed on the node, with a mean of 64.9 million years ago (mya) and a standard deviation of 10 mya. In all analyses, an uncorrelated lognormal relaxed clock model was estimated independently for each gene. The clock means for each gene (except for ND1 in the mtDNA rate calibrated analysis) were assigned exponential distributions with a mean of 1.0, whereas the standard deviations were assigned exponential distributions with a mean of 0.05. These analyses were run for 100 million generations, sampling every 8,000 generations. Convergence was assessed using Tracer (Drummond and Rambaut, 2007), thereby assuring that all parameters had reached stationarity and sufficiently effective (> 200) sample sizes. Both calibration strategies produced similar age estimates, and the results from the point calibration are shown in Figure 8.3.

Statistical Analyses

Most statistical analyses of morphometric and coded morphological and color characters were accomplished on a Honeywell 66/60 mainframe computer at the Academic Computing Center, University of Kansas. The statistical analyses of morphometric data were done through the use of the BioMeDical Package (BMDP) computer programs (Dixon, 1981). Univariate statistics (BMDP2D) and one-way analyses of variances, including tests for the homogeneity of variances (ANOVA; BMDP7D), were applied only to adults separated by sex. Principal components analyses (variance-covariance matrix; BMDP4M) of transformed ($\log_{10}$) morphometric data were used as a preliminary test to ensure that the combined data for the sexes could be analyzed as a single group. Subsequently, stepwise discriminant analyses (BMDP7M) were performed on transformed ($\log_{10}$) data with the sexes combined and subadults included.

Data for external descriptive characters and color pattern characters were recorded in a dichotomous fashion—i.e., presence or absence of a character state. Data taken in this manner enabled the application of multivariate statistical analyses (Maxwell, 1961; Blackith and Reyment, 1971). Data on descriptive characters were subjected to cluster analyses, according to unweighted pair-group matching based on squared Euclidean distances, using the CLUSTAN software package (Wishart, 1978).

Illustrations

The drawings of whole animals or parts thereof were done with the aid of a Wild M-8 Stereozoom binocular microscope with a camera-lucida drawing attachment. The photographs of embryos and histological preparations were taken with a Nikomat 35 mm automatic photographic attachment for the same microscope. My photographs of living frogs in the field were taken on Kodachrome-64 35 mm film. More recent photos by colleagues were taken with digital cameras. Images of their photographs are deposited in the open access University of Kansas Digital Archives (KUDA) in the Division of Herpetology, Biodiversity Institute, University of Kansas; all such photographs are acknowledged by KUDA in their legends. Permissions were obtained for copyrighted images by Manuella Folly, Philippe J. R. Kok, Edgar Lehr, Cyro de Luna-Dias Neto, Mauro Teixeira Jr., and Vivian Trevine.

The maps were generated using ArcGIS, version 9. The topographic data are based on a digital elevation model of the globe at 90 m spatial resolution, provided by the CGIAR Consortium for Spatial Information (www.cgiar-csi.org). The continuous elevation data were binned into 500–1000 meter categories to simplify their presentation. The spatial reference data for administrative units (state and country boundaries) and water features were obtained from the DIVA-GIS free spatial-data website (www.diva-gis.org). All maps were processed in Adobe Illustrator CS5.

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2

The Place of Hemiphractids in Anuran Phylogeny

Much of contemporary biology is dependent upon the phylogenetic relationships of organisms. Thus, in order to understand the evolutionary significance of the morphological attributes and unique reproductive modes of marsupial frogs and their allies, it is necessary to examine them in the context of their phylogenetic history. The three earliest-known species now regarded as marsupial frogs or their allies are *Rana scutata* Spix, 1824 [= *Hemiphractus scutatus*], *Hyla marsupiata* Duméril and Bibron, 1841 [= *Gastrotheca marsupiata*], and *Notodelphys ovifera* Lichtenstein and Weinland, 1854 [= *Gastrotheca ovifera*]. Soon after these names were published, new genera were proposed: *Hemiphractus* Wagler, 1828, for *Rana scutata* and *Gastrotheca* for *Hyla marsupiata*. *Notodelphys* was preoccupied (i.e., not available because of prior publication), so Günther (1859) proposed *Opisthodelphys* as a substitute name. Many different phylogenetic schemes of the relationships of marsupial frogs and their allies are reflected in the changing classifications that appeared in the nineteenth and most of the twentieth centuries, but they all shared one feature in common—they were based primarily on morphological characters, although life-history data became an important aspect in the twentieth century (e.g., Noble, 1927).

Morphological Phylogenetic Analyses

Workers in the nineteenth century mainly relied on the similarity of external morphological characters for the placement of taxa in anuran classifications. Wagler (1828, 1830) described and illustrated the morphologically bizarre *Hemiphractus scutatus* and contended that it had mandibular teeth. Günther (1859) considered *Hemiphractus* to be a junior synonym of *Ceratophrys*, which was placed in Ranidae. *Hemiphractus* probably was grouped with *Ceratophrys*, because both possess odontoids on the mandibles. Günther also used *Nototrema* as a substitute name for *Gastrotheca marsupiata* and placed both that species and *Opisthodelphys ovifera* in Hylidae, which he characterized as having webbed toes, dilated processes of the sacral vertebrae, and no parotoid glands.

A few years later Peters (1862) proposed that *Hemiphractus* was related to the hylid tree frogs and erected the family Hemiphractidae, which he distinguished from other anuran families by the following combination of characters: (1) the absence of parotoid glands; (2) the presence of small transverse processes of the sacral vertebrae; (3) the presence of "teeth" on the palatine (= neopalatine) bones (not actually teeth, but bony serrations); (4) the presence of rudimentary digital webbing; (5) the presence of a round attached tongue; and (6) the presence of "flattened digital tips" (presumably he was referring to the bottoms of the digits being flat). In his major classification of frogs, Cope (1866) retained *Gastrotheca* and *Opisthodelphys* in Hylidae. In his third group of frogs with arciferal pectoral girdles, cylindrical sacral diapophyses, and proceolous vertebrae, he recognized two families, Hemiphractidae and Cystignathidae [= Leptodactylidae, sensu lato]. Hemiphractidae was distinguished from Cystignathidae by the presence of mandibular teeth (= odontoids) in the former and their absence in the latter.

Jiménez de la Espada (1871) proposed the generic name *Cerathyla* for four new species of hemiphractid frogs from Ecuador and noted that *Cerathyla* was "hylid-like," whereas *Hemiphractus* was stockier and "toad-like." Brocchi (1877) published osteological details of *H. scutatus* and correctly stated that it possessed odontoids, not true teeth, on the mandible. In his great compendium on frogs, Boulenger (1882) placed *Nototrema* [= *Gastrotheca*] in Hylidae. He recognized Hemiphractidae as containing *Ceratohyla*, *Hemiphractus*, and *Amphodus* [= *Phyllodytes*] and described a new family, Amphignathodontidae, for *Amphignathodon guentheri*, which has true teeth on the mandible. Boettger (1893) described *Nototrema* [= *Flectonotus*] *pygmaeus*, a small marsupial frog from Venezuela possessing a dorsal brood pouch with a longitudinal opening. Several additional species of *Nototrema* [= *Gastrotheca*] were described in the 1880s and 1890s. Thus, by the end of the nineteenth century, marsupial frogs and their allies were separated into three families: Hemiphractidae, with 5 species of *Cerathyla* and 1 species of *Hemiphractus*; Hylidae, with 11 species of *Nototrema* [= *Flectonotus* and *Gastrotheca*]; and Amphignathodontidae, with *Amphignathodon guentheri*.

Early in the twentieth century, Gadow (1901) recognized these genera as constituting the subfamily Hemiphractinae in Cystignathidae [= Leptodactylidae, sensu lato], but otherwise accepted Amphignathodontidae and the placement of *Nototrema* [= *Flectonotus* and *Gastrotheca*] in Hylidae. There was also the notable addition of *Cryptobatrachus* by Ruthven (1916). Earlier, Ruthven (1915) had noted the sheet-like external gills on young hatching from eggs on the backs of females of *Hyla* [= *Cryptobatrachus*] *fuhrmanni*, described by Peracca in 1914. Ruthven (1922) later placed *H. goeldii* and *H. evansi* (described by Boulenger [1895, 1904] from Brazil and British Guiana, respectively) in *Cryptobatrachus*. Ruthven (1916, 1922) considered *Cryptobatrachus* to be in Cystignathidae [= Leptodactylidae, sensu lato].

Noble (1926) placed *Cerathyla* in the synonymy of *Hemiphractus* and subsequently proposed the subfamilial name Gastrothecinae for *Amphignathodon*, *Cryptobatrachus*, *Gastrotheca*, and *Hemiphractus* (Noble, 1927), emphasizing that all of these frogs have embryos with large bell-shaped gills. This is the first all-inclusive feature related to developmental morphology noted for the marsupial frogs and their allies. Throughout most of the twentieth century, marsupial frogs and their relatives were thought to be hylid frogs, variously recognized as belonging to Amphignathodontinae (*A. guentheri*) and Hemiphractinae. Goin (1961) presented a synopsis of Hylidae, in which he included *Amphignathodon*, *Cerathyla*, *Cryptobatrachus*, *Flectonotus*, *Fritziana*, *Gastrotheca*, *Hemiphractus*, and *Nototheca* in the family. Duellman (1970) placed all of the egg-brooding hylid frogs in Amphignathodontinae, which was deemed to be separate from Hemiphractinae. Trueb (1974) maintained this arrangement but emphasized that the two subfamilies represented a single phyletic line (i.e., a clade). Using immunological distances, Duellman et al. (1988) showed *Amphignathodon* to be nested within *Gastrotheca*, thus rendering it paraphyletic; consequently *Amphignathodon* was placed in the synonymy of *Gastrotheca*.

Rivero (1968) concluded that *Cryptobatrachus evansi* was generically distinct and erected the genus *Stefania* for that species and four others in the Guiana Highlands. Duellman and Hoogmoed (1984) added two more species to the genus and provided a phylogenetic arrangement, based on morphological and developmental characters, in which *Cryptobatrachus* and *Stefania* form a clade that is most closely related to *Hemiphractus*. Subsequent exploration of the Guiana Highlands has revealed the existence of 12 additional species of *Stefania* (Myers and Donnelly, 1997; Señaris et al., 1997; MacCulloch and Lathrop, 2002; Barrio-Amorós and Fuentes, 2003; Carvalho et al., 2010).

The most unusual classification and proposed phylogeny, based on morphological and developmental characters, is that of Lutz (1968), who ignored earlier familial names and proposed the hylid subfamily Opisthodelphyinae for all of the frogs formerly placed in Amphignathodontinae and Hemiphractinae (Fig. 2.1). She characterized the family as being the Neotropical

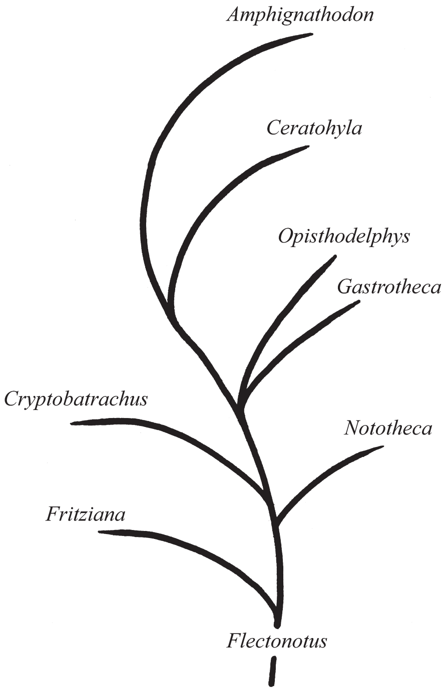

Fig. 2.1 Hypothesized relationships of the genera of Opisthodelphyine hylid frogs recognized by Lutz (1968).

hylids in which "the female carries her developing spawn on her back" and "the known embryos exhibit peculiar handkerchief-like gills" (Lutz, 1968:16). She also stated: "One more genus, *Hemiphractus*, generally is included in this group. I have left it out, as it seems very doubtful that this small-disked frog, living like an *Eleutherodactylus*, really is a hylid." To my knowledge, no subsequent worker accepted Lutz's arrangement.

In the most recent phylogenetic analysis of morphological and developmental characters of hylid frogs, Duellman (2001) used 10 osteological characters, the pupil shape, 10 myological characters, the chromosome number, and 2 developmental features in a parsimony analysis. A hypothetical bufonoid frog having primitive states for all characters was used as the outgroup, and Centrolenidae and *Allophryne ruthveni* were included in the analysis. Three equally parsimonious trees were consistent with respect to Hylidae, in which Phyllomedusinae and Hemiphractinae were sister-groups (Fig. 2.2), supported by two unique morphological transformations (the proximal head of Metacarpal II not between the prepollex and the distal prepollex, and the larval spiracle ventrolateral in position). Hemiphractines also have the plesiomorphic diploid chromosome number (2*n*) 26, a character shared with Pelodryadinae and Phyllomedusinae. Burton

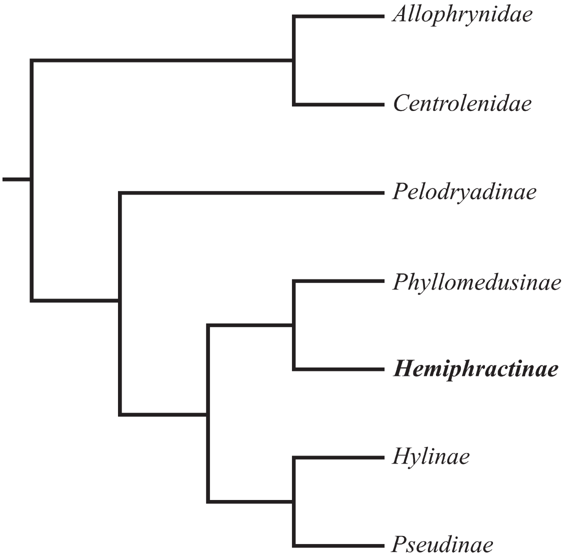

Fig. 2.2 Phylogenetic tree of Hylidae and related families, based on morphology in which Hemiphractidae is placed as a subfamily of Hylidae. Duellman (2001) and Burton (2004).

(2004) supported this phylogenetic arrangement by an additional 32 myological characters.

Not all phylogenetic studies produced the same results. For example, Hass (2003) used 156 larval characters of 81 taxa of frogs in a parsimony analysis that resulted in his single example of a hemiphractine (*Gastrotheca riobambae*) being a sister taxon to ranoid frogs in some analyses, whereas all other hylids formed a monophyletic group. The evidence was not robust, and the arrangement collapsed when morphometric characters were included, such that *G. riobambae* was in a polytomy with four leptodactylids and five ranids. Thus Haas concluded that the relationships of hemiphractines remained enigmatic. The only other morphological analysis was that of Mendelson et al. (2000), who assumed that Hemiphractinae was monophyletic. Many of the characters used covary with hyperossification of the cranial elements; thus they greatly multiplied the number of cranial characters, which led to the implausible placement of *Hemiphractus* within *Gastrotheca*.

Molecular Phylogenetic Analyses

Although Scanlan et al. (1980) and Duellman et al. (1988) used immunological distances and Duellman and Hillis (1987) analyzed allozymes in attempts to uncover phylogenetic relationships within *Gastrotheca*, the earliest inference of phylogenetic relationships

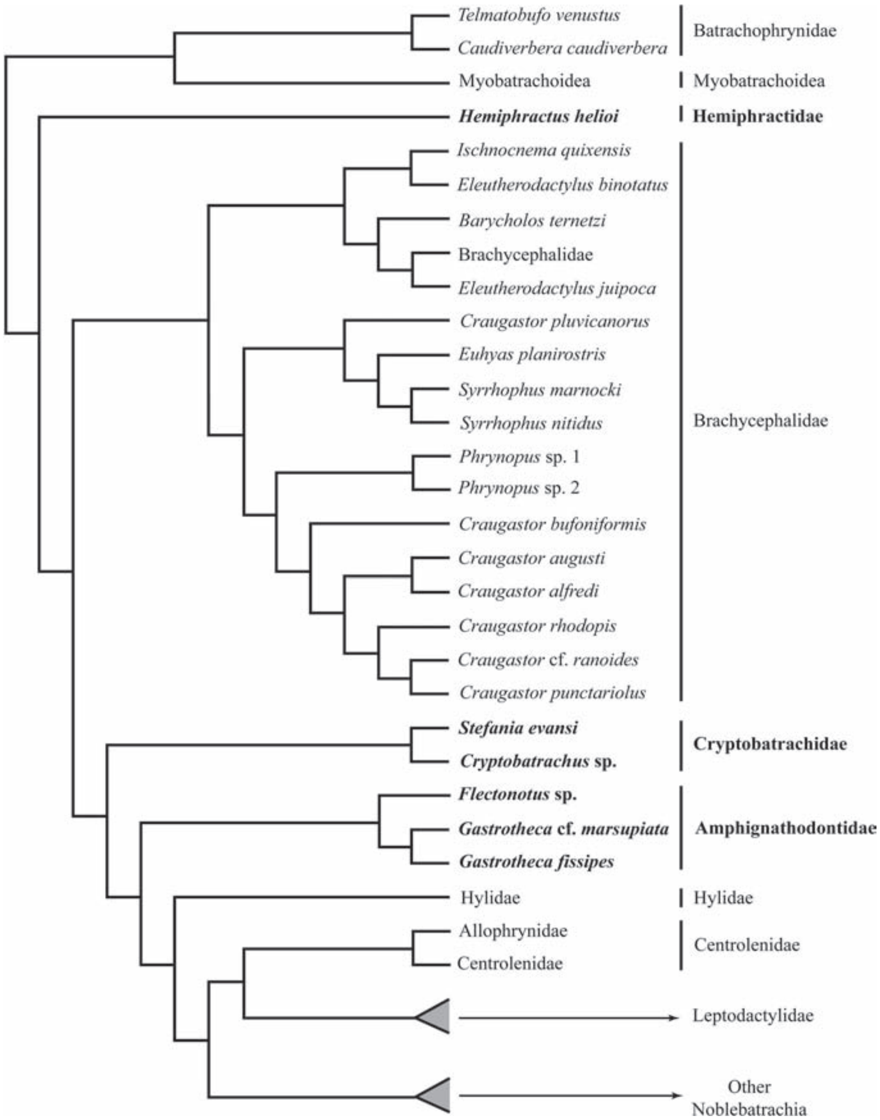
Telmatobufo venustus
Caudiverbera caudiverbera
Batrachophrynidae
Myobatrachoidea
Myobatrachoidea
Hemiphractus helioi
Hemiphractidae
Ischnocnema quixensis
Eleutherodactylus binotatus
Barycholos ternetzi
Brachycephalidae
Eleutherodactylus juipoca
Craugastor pluvicanorus
Euhyas planirostris
Syrrhophus marnocki
Syrrhophus nitidus
Brachycephalidae
Phrynopus sp. 1
Phrynopus sp. 2
Craugastor bufoniformis
Craugastor augusti
Craugastor alfredi
Craugastor rhodopis
Craugastor cf. ranoides
Craugastor punctariolus
Stefania evansi
Cryptobatrachus sp.
Cryptobatrachidae
Flectonotus sp.
Gastrotheca cf. marsupiata
Gastrotheca fissipes
Amphignathodontidae
Hylidae
Hylidae
Allophrynidae
Centrolenidae
Centrolenidae
Leptodactylidae
Other Noblebatrachia

Fig. 2.3 Placement of marsupial frogs and their allies (in boldface) in the parsimony analysis of two mitochondrial and two nuclear genes. *Right-hand column*: family designations. Frost et al. (2006).

based on DNA sequences was by Ruvinsky and Maxson (1996). Their analysis of 12S and 16S mitochondrial genes of 30 species included only one hemiphractine, *Gastrotheca riobambae*. In the resulting tree, *Gastrotheca* is the sister taxon to *Bufo*, which together are allied with Centrolenidae. Darst and Cannatella (2004), also relying on sequence data from 12S and 16S mitochondrial genes from 93 species of neobatrachian frogs, included only two hemiphractines, *Cryptobatrachus* sp. and *Gastrotheca pseustes*. Their results provided weak support that Hemiphractinae is polyphyletic, with *Cryptobatrachus* associated with eleutherodactylines and *Gastrotheca* imbedded in a group of leptodactyline frogs.

In 2005 two completely independent phylogenetic arrangements of hylid frogs were published. The most extensive molecular dataset of hylid frogs was the exhaustive study by Faivovich et al. (2005). They employed sequences of four mitochondrial and five nuclear genes in a parsimony analysis of 228 species of hylid frogs; the dataset included many partial sequences obtained from GenBank and included nine hemiphractine frogs. Their results indicated that the hemiphractines that were analyzed did not form a monophyletic group and were not contained in Hylidae; the authors tentatively placed Hemiphractinae in the paraphyletic Leptodactylidae. In contrast, Wiens et al. (2005) ran independent and combined analyses of 2 mitochondrial genes, 2 nuclear genes, and 144 morphological characters of 169 species of hylids,

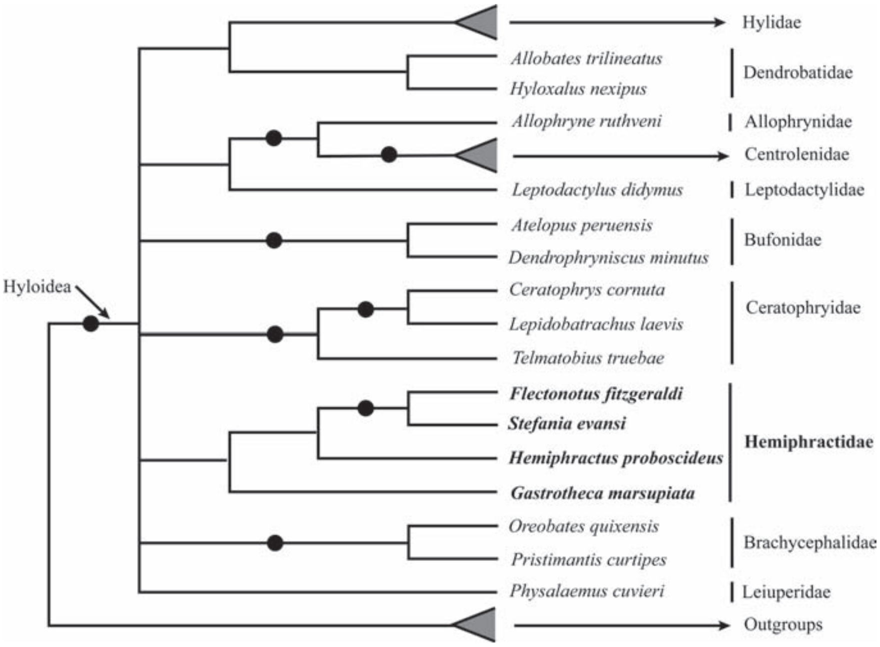
Hylidae
Allobates trilineatus
Hyloxalus nexipus
Dendrobatidae
Allophryne ruthveni
Allophrynidae
Centrolenidae
Leptodactylus didymus
Leptodactylidae
Atelopus peruensis
Dendrophryniscus minutus
Bufonidae
Hyloidea
Ceratophrys cornuta
Lepidobatrachus laevis
Telmatobius truebae
Ceratophryidae
Flectonotus fitzgeraldi
Stefania evansi
Hemiphractus proboscideus
Gastrotheca marsupiata
Hemiphractidae
Oreobates quixensis
Pristimantis curtipes
Brachycephalidae
Physalaemus cuvieri
Leiuperidae
Outgroups

Fig. 2.4 Consensus tree, based on mitochondrial and nuclear genes. Black circles indicate significant support in Bayesian, maximum likelihood, and maximum parsimony analyses. Guayasmin et al. (2008).

including 7 species of 5 genera of hemiphractines. The data were subjected to various parsimony and Bayesian analyses. With the exception of the analysis of only morphological characters, the hemiphractines appeared as a monophyletic group associated with the "leptodactylid" genera *Eleutherodactylus*, *Ischnocnema* [= *Oreobates*], and *Phrynopus*. Consequently, Wiens et al. (2007) recognized Hemiphractidae as a family not associated with Hylidae.

A publication by Frost et al. (2006), purported to be "the amphibian tree of life," was based primarily on molecular data (two mitochondrial and five nuclear genes maximum, although the mitochondrial genes essentially represented a single genetic locus) and larval characters taken from Haas (2003). Using the results of parsimony analysis for 519 species of amphibians, Frost et al. (2006) proposed a radical new classification of living amphibians. As might be expected in an analysis using fewer than 9% of the recognized species, the phylogenetic arrangement and subsequent classification in some places are chaotic. This is especially so in the case of hemiphractid frogs, where six species of five genera were included. Frost et al. sampled fewer hemiphractid taxa than Faivovich et al. (2005) and came to far different conclusions. Whereas Faivovich et al. concluded that their samples of marsupial frogs and allied genera formed a monophyletic group, in the consensus tree created by Frost et al. (2006), *Hemiphractus helioi* is recognized as part of Hemiphractidae and is the sister taxon to a group of species of direct-developing frogs placed in Brachycephalidae. One separate lineage containing *Cryptobatrachus* and *Stefania* is designated Cryptobatrachidae, and another consisting of *Flectonotus* and two species of *Gastrotheca* is designated the Amphignathodontidae; only the latter is distantly allied with Hylidae (Fig. 2.3) (see page 17). Ironically, this immense study has marsupial frogs and their allies placed in about the same way they were at the end of the nineteenth century!

In a study based on mitochondrial and nuclear genes, Guayasamin et al. (2008) recovered a clade with significant support that included all marsupial frogs in phylogenetic analyses of nuclear and nuclear plus mitochondrial data, but not when the mitochondrial data were analyzed alone. Thus they concluded that Amphignathodontidae, Cryptobatrachidae, and Hemiphractidae form a monophyletic group, which they referred to Hemiphractidae (Fig. 2.4). A similar analysis of 45 species of marsupial frogs by Wiens et al. (2007) revealed Hemiphractidae to be monophyletic. Thus, in the first nine years in the twenty-first century, the marsupial frogs and their allies have been classified as a subfamily of Hylidae (Duellman, 2001); a subfamily of Leptodactylidae (Faivovich et al., 2005); a single monophyletic family, Hemiphractidae (Wiens et al., 2007; Guayasamin et al., 2008); and three families—Amphignathodontidae, Cryptobatrachidae, and Hemiphractidae (Frost et al., 2006). Despite all of these analyses, the placement of these genera in the overall phylogeny of anurans remained unresolved.

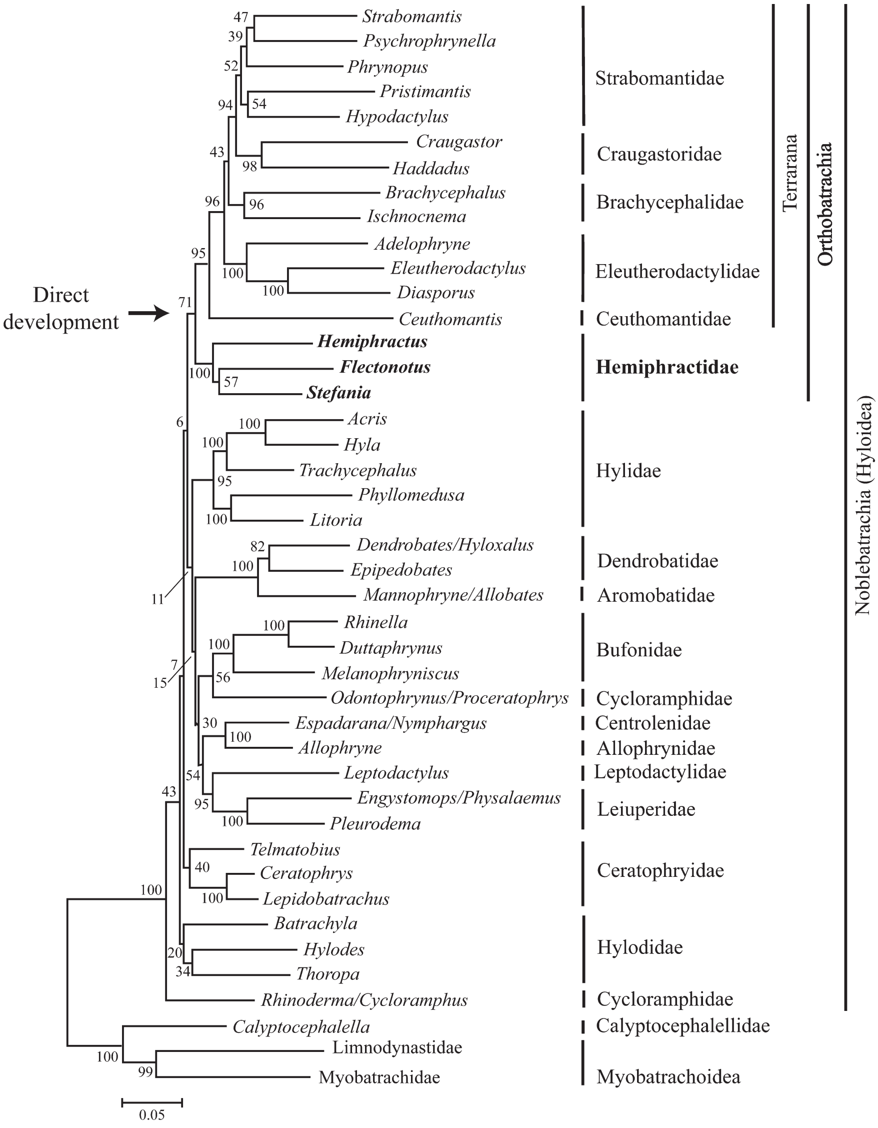
Strabomantis
Psychrophrynella
Phrynopus
Pristimantis
Hypodactylus
Craugastor
Haddadus
Brachycephalus
Ischnocnema
Adelophryne
Eleutherodactylus
Diasporus
Ceuthomantis
Hemiphractus
Flectonotus
Stefania
Acris
Hyla
Trachycephalus
Phyllomedusa
Litoria
Dendrobates/Hyloxalus
Epipedobates
Mannophryne/Allobates
Rhinella
Duttaphrynus
Melanophryniscus
Odontophrynus/Proceratophrys
Espadarana/Nymphargus
Allophryne
Leptodactylus
Engystomops/Physalaemus
Pleurodema
Telmatobius
Ceratophrys
Lepidobatrachus
Batrachyla
Hylodes
Thoropa
Rhinoderma/Cycloramphus
Calyptocephalella
Limnodynastidae
Myobatrachidae
Strabomantidae
Craugastoridae
Brachycephalidae
Eleutherodactylidae
Ceuthomantidae
Hemiphractidae
Hylidae
Dendrobatidae
Aromobatidae
Bufonidae
Cycloramphidae
Centrolenidae
Allophrynidae
Leptodactylidae
Leiuperidae
Ceratophryidae
Hylodidae
Cycloramphidae
Calyptocephalellidae
Myobatrachoidea
Terrarana
Orthobatrachia
Noblebatrachia (Hyloidea)
Direct development
0.05

Fig. 2.5 Phylogenetic tree (maximum likelihood) of hyloid frogs, based on 17 genes of selected genera. Bootstrap support values are indicated at the nodes. Modified from Heinicke et al. (2009).

Frogs formerly placed in the immense, diverse genus *Eleutherodactylus* were subjected to phylogenetic analyses of two mitochondrial and two nuclear genes by Hedges et al. (2008). Their analysis of 344 species resulted in the recognition of four families (Brachycephalidae, Craugastoridae, Eleutherodactylidae, and Strabomantidae) that are placed in the unranked taxon Terrarana; this taxon includes nearly all of the New World frogs that have direct development of eggs deposited on the ground or on vegetation. In allocating a new terraranan, Heinicke at al. (2009) used 11 nuclear and 6 mitochondrial genes in an analysis of the new taxon (*Ceuthomantis*) and 43 other anuran taxa, including all hyloid families (Noblebatrachia of Frost et al., 2006) and three hemiphractids. For both full and limited alignments, the maximum likelihood, maximum parsimony, and Bayesian analyses supported both the position of the new taxon as the closest relative of Terrarana and marsupial frogs as the closest relatives of the expanded Terrarana (Fig. 2.5). This arrangement was modified in a weakly supported arrangement of the terraranans being basal to Hemiphractidae and Hylidae (Pyron and Wiens, 2011).

Heinicke et al. (2009) proposed the unranked taxon Orthobatrachia for Hemiphractidae + Terrarana. Their Bayesian molecular clock analysis showed the divergence between Terrarana and Hemiphractidae to be approximately 65 (48–89) million years ago. This suggests that at least terrestrial reproduction, if not direct development, had evolved among South American frogs by the Late Cretaceous and provides a starting point for the evolution of the unique reproductive mode of hemiphractid frogs, a lineage that now seems to have found its place in anuran phylogeny and classification.

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3

Phylogeny and Classification

Herein I present a hypothesis based on molecular data of the relationships of the marsupial frogs and their allied genera; the classification given is derived from this analysis. An analysis of combined molecular and morphological data (chapter 4) agrees in general with the broad scheme of relationships derived from the molecular data but differs in the placement of a few taxa in the subgenera *Duellmania* and *Gastrotheca*: *G. bufona*, *ovifera*, and *phalarosa*. The reader well may ask why I present the tree based on molecular data in preference to that based on combined data. The answer is not elegant, but practical. Lacking a concordance of samples (i.e., molecular and morphological data on the same set of taxa), I chose the most inclusive and complete dataset—i.e., the one having the greatest number of taxa—and the one with the least-obvious homoplasy.

Phylogenetic Relationships

Early hypotheses of phylogenetic relationships among hemiphractid frogs were based mostly on morphological similarities (e.g., Fig. 2.1; Lutz, 1968). Attempts to ascertain phylogenetic relationships using the programs PAUP* 4.0 (Swofford, 2003), GARLI (Zwickl, 2006), and MacClade (Maddison and Maddison, 2011) on osteological and external morphological datasets proved to be of limited use, because of the great amount of homoplasy; nonetheless, some clades were recognized.

The first phylogeny of *Gastrotheca* was proposed by Wiens et al. (2007), who used a maximum of three mitochondrial and two nuclear genes in an analysis of 34 species of *Gastrotheca* and 11 species of other genera of hemiphractids. The analysis disclosed *Stefania* to be the sister-group to *Gastrotheca* and *G. fissipes* to be the basal species within *Gastrotheca*. In addition to that basal taxon, the analysis revealed three major clades; two of these lineages included species producing tadpoles, along with others having direct development. Blackburn and Duellman (2013), who analyzed the states of two mitochondrial and two nuclear genes of 50 species of *Gastrotheca* and 14 other hemiphractids, expanded on the work of Wiens et al. (2007) and showed that there was strong support for six major geographically circumscribed lineages.

Herein, the same genes (see chapter 1, "Materials and Methods") were used to generate a phylogenetic arrangement of 62 species of *Gastrotheca* and 15 species representing the other genera of hemiphractid frogs (Fig. 3.1). Seven unnamed species of *Gastrotheca* are included in the analysis; thus the results show proposed relationships of 55 of the 69 (80%) species of *Gastrotheca*. Data from only one specimen per species were used for the construction of the tree. In those cases in which genetic data were available for more than one specimen of a given species, selection of the individual used in the tree was determined by (1) the number of genes that were sequenced, (2) geographic proximity to the type locality, (3) closeness to the mean genetic distance when three or more individuals were involved, or (4) any combination of the foregoing criteria. The monophyly of five of the six genera of hemiphractid frogs is strongly supported by bootstrap values of 95% or higher; the monophyly of *Cryptobatrachus* could not be ascertained, because only one species was included in the analysis.

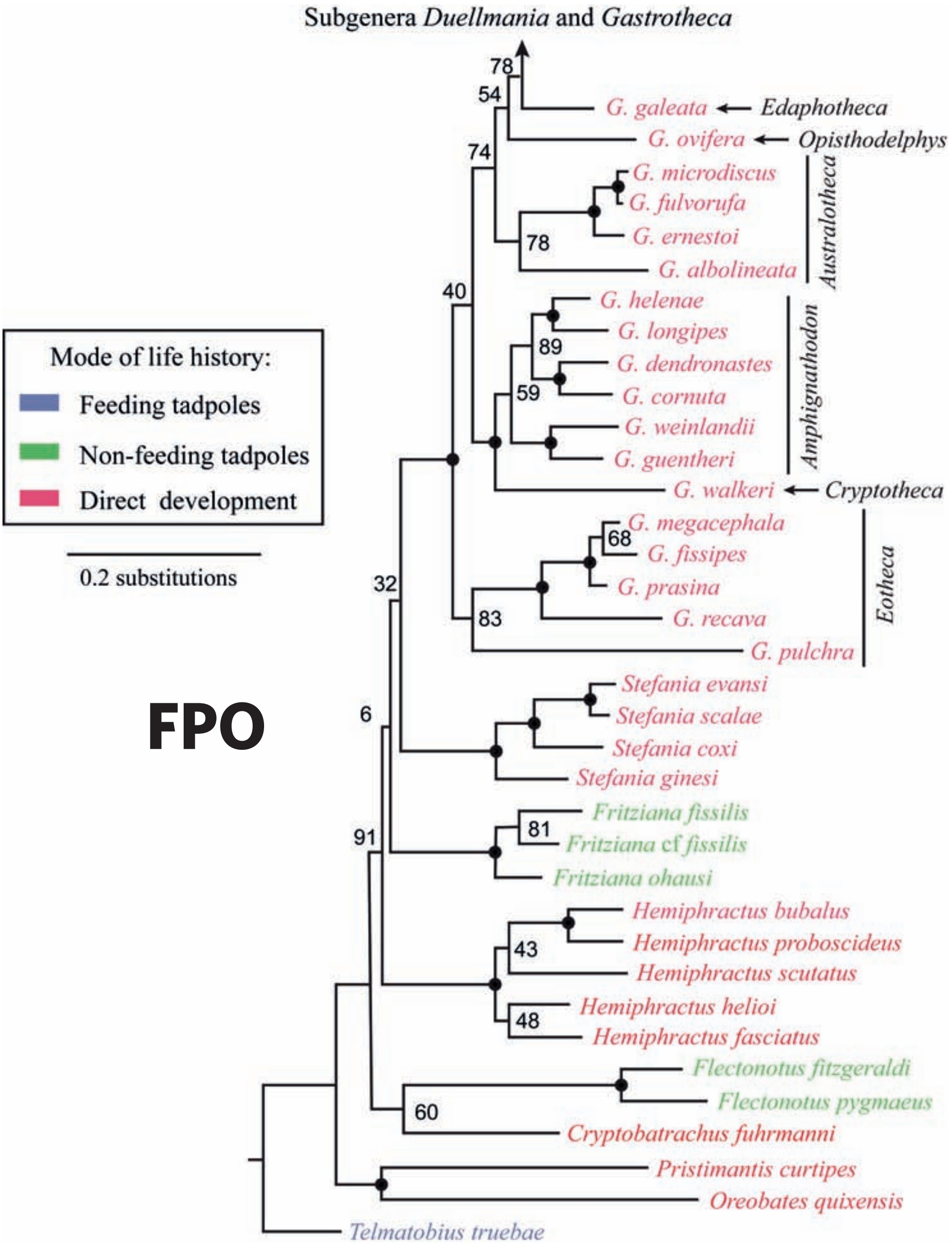
The basal position of *Cryptobatrachus* and *Flectonotus* is supported by shared characteristics of their reproductive biology (chapter 7). The monophyly of *Hemiphractus* is supported by many osteological characters (Trueb, 1974), which, in combination with the genetic data, reject the proposal by Mendelson et al. (2000) that *Hemiphractus* is imbedded within *Gastrotheca*. Results of earlier phylogenetic analyses (e.g., Duellman and Gray, 1983) placed *Flectonotus* and *Fritziana* in one genus. Members of both genera are unique among hemiphractids in their possession of non-feeding tadpoles, but as shown by Duellman et al. (2011), the two genera are not closely related genetically; furthermore, they differ in their morphology and reproductive biology. Primarily based on their morphological similarities, frogs of the genera *Cryptobatrachus* and *Stefania* were considered to be sister taxa (Rivero, 1968; Duellman and Hoogmoed, 1984). Genetic data reveal that they are not closely related; their genetic distance is supported by morphological features unique to *Cryptobatrachus* (Lynch, 2008). Even though the monophyly of all of the genera is strongly supported, in some cases their relationships with one another are weakly supported (e.g., the placement of *Fritziana* and *Hemiphractus*).

As shown in Figure 3.1, *Gastrotheca* is the most derived and speciose genus in Hemiphractidae. Blackburn and Duellman (2013) identified six clades in *Gastrotheca* and emphasized circumscribed geographic ranges for each clade. Herein, I recognize eight monophyletic lineages within *Gastrotheca*, and these clades are recognized as subgenera (Fig. 3.1). The basal clades inhabit lowland forests in eastern Brazil (*Australotheca* and *Eotheca*) and northwestern South America, and cloud forests and humid montane forests in the Andes and highlands of lower Central America and northern Venezuela (*Amphignathodon*, *Cryptotheca*, *Edaphotheca*, and *Opisthodelphys*). The two largest clades (*Duellmania* and *Gastrotheca*) inhabit puna, páramo, and subpáramo at higher elevations in the Andes from northern Colombia to northern Argentina.

Like most of the other genera of hemiphractids, the basal clades of *Gastrotheca* (*Amphignathodon*, *Australotheca*, *Cryptotheca*, *Edaphotheca*, *Eotheca*, and *Opisthodelphys*) produce eggs that undergo direct development. Thus the reproductive pattern of producing eggs that hatch as tadpoles is a derived feature in the Andean subgenera *Duellmania* and *Gastrotheca*. The immediate ancestor to these subgenera is *Gastrotheca* (*Edaphotheca*) *galeata*, a species having direct development.

The common ancestor to the subgenus *Duellmania* had free-living tadpoles. All but three of the species in this clade produce eggs that hatch as tadpoles; the tadpoles of three species in the larger group (*Gastrotheca argenteovirens*, *dunni*, and *trachyceps*) hatch at developmental Stages 37–39 (Gosner, 1960), whereas the others hatch at Stages 30–31. The remaining three species in this subgenus have direct development (Fig. 3.2). Molecular, morphological, and reproductive data show that two of these (*G. orophylax* and *G. plumbea*) are sister taxa. The embryos of *G. orophylax* have a nearly complete set of larval mouthparts, exclusive of keratinized beaks (Wassersug and Duellman, 1984), and embryos in advanced stages of development that have been removed from their egg capsules can complete their development (chapter 7). The third member of the subgenus having direct development (*G. nicefori*) is an enigma. In the phylogenetic tree based on molecular data, *G. nicefori* is nestled among the tadpole-producing species in the northern clade of *Duellmania*, but it differs from all other members of the subgenus by being about 15 mm larger (snout–vent length) than any of the others. Moreover, it is the only species in the subgenus having a transverse occipital crest and the skin of the skull co-ossified with the underlying bones. In general appearance it resembles some species in the subgenus *Amphignathodon*.

The common ancestor to the subgenus *Gastrotheca* apparently had direct development. With the exception


Subgenera Duellmania and Gastrotheca
Mode of life history:
Feeding tadpoles
Non-feeding tadpoles
Direct development
0.2 substitutions
FPO
78
54
74
40
78
89
59
32
68
83
6
91
81
43
48
60
G. galeata ← Edaphotheca
G. ovifera ← Opisthodelphys
G. microdiscus
G. fulvorufa
G. ernestoi
G. albolineata
Australotheca
G. helenae
G. longipes
G. dendronastes
G. cornuta
G. weinlandii
G. guentheri
Amphignathodon
G. walkeri ← Cryptotheca
G. megacephala
G. fissipes
G. prasina
G. recava
G. pulchra
Eotheca
Stefania evansi
Stefania scalae
Stefania coxi
Stefania ginesi
Fritziana fissilis
Fritziana cf fissilis
Fritziana ohausi
Hemiphractus bubalus
Hemiphractus proboscideus
Hemiphractus scutatus
Hemiphractus helioi
Hemiphractus fasciatus
Flectonotus fitzgeraldi
Flectonotus pygmaeus
Cryptobatrachus fuhrmanni
Pristimantis curtipes
Oreobates quixensis
Telmatobius truebae

of the outlying *G. zeugocystis*, which has direct development, three major clades have weak support values; they also inhabit different geographic regions of the Andes. The northernmost group (southern Ecuador to central Peru) contains eight named and six unnamed species; for those of which the life histories are known, the eggs hatch as tadpoles. The sister clade consists of species from the Andes in Peru; all have direct development. The sister-group to those two clades is composed of some species with direct development and some with free-living tadpoles. The sister taxa *G. griswoldi* (direct development) and *G. marsupiata* (tadpoles) exist, respectively, in the Andes in central Peru and in southern Peru and adjacent Bolivia. The other members of this clade occur in central Bolivia and northern Argentina; two of the latter have tadpoles, whereas the others undergo direct development.

Based on the phylogenetic arrangement presented here, a life history with direct development is basal in the genus *Gastrotheca*. Production of eggs that hatch

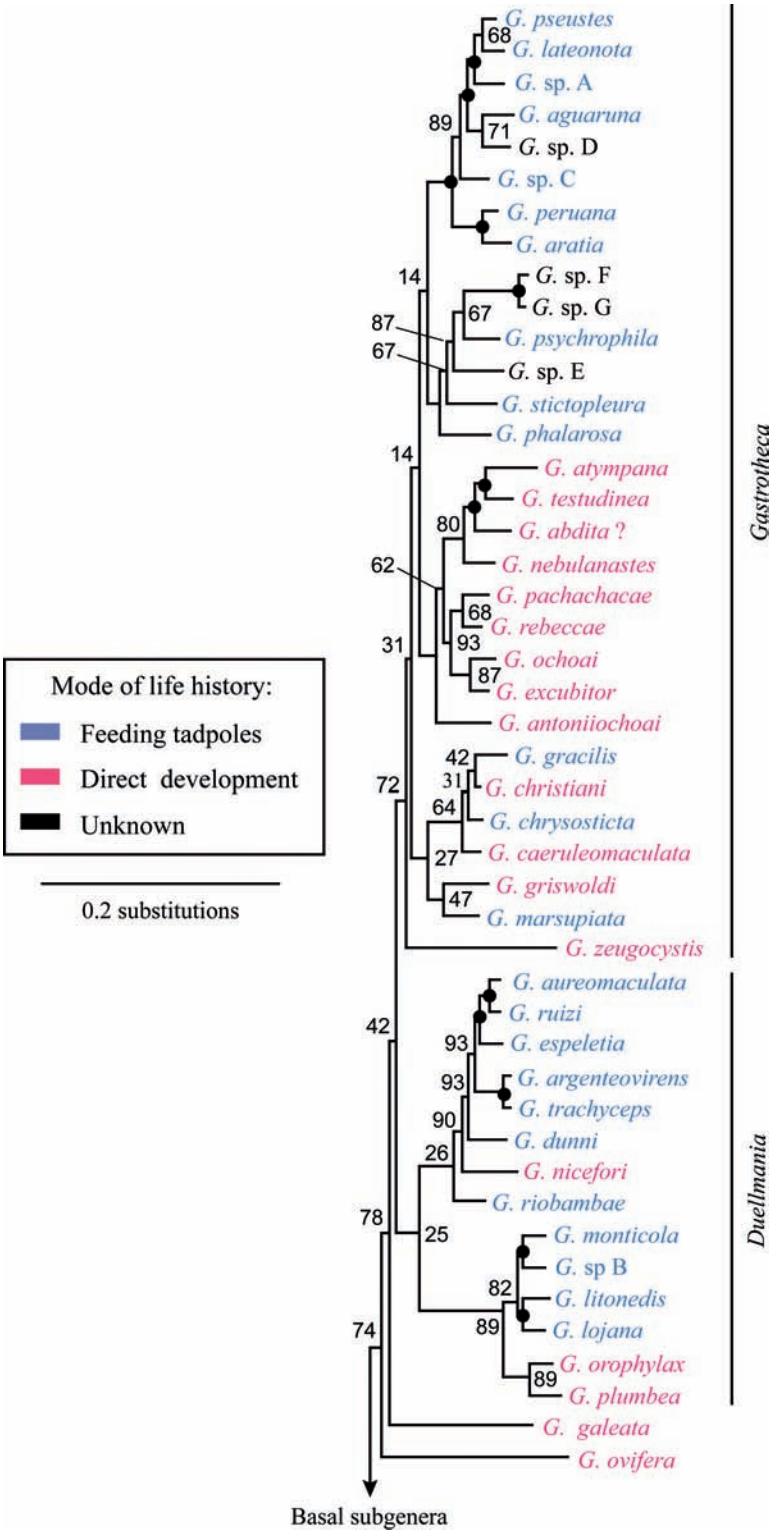

G. pseustes
68
G. lateonota
G. sp. A
89
G. aguaruna
71
G. sp. D
G. sp. C
G. peruana
G. aratia
14
G. sp. F
G. sp. G
87
67
G. psychrophila
67
G. sp. E
G. stictopleura
G. phalarosa
14
G. atympana
G. testudinea
80
G. abdita ?
G. nebulanastes
62
G. pachachacae
68
G. rebeccae
93
31
G. ochoai
87
G. excubitor
G. antoniiochoai
42
G. gracilis
31
G. christiani
64
72
G. chrysosticta
27
G. caeruleomaculata
G. griswoldi
47
G. marsupiata
G. zeugocystis
Gastrotheca
G. aureomaculata
G. ruizi
42
93
G. espeletia
93
G. argenteovirens
G. trachyceps
90
G. dunni
26
G. nicefori
G. riobambae
78
25
G. monticola
G. sp B
82
G. litonedis
74
89
G. lojana
G. orophylax
89
G. plumbea
G. galeata
G. ovifera
Duellmania
Basal subgenera
Mode of life history:
Feeding tadpoles
Direct development
Unknown
0.2 substitutions

Fig. 3.1 Maximum likelihood phylogeny depicting inferred relationships among marsupial frogs and their allies, based on two nuclear and two mitochondrial genes. Nodes with high support (≥ 95) are indicated by black circles, and support values (using 1000 bootstrap replicates) are indicated on other selected nodes. Species are color coded by their mode of life history.

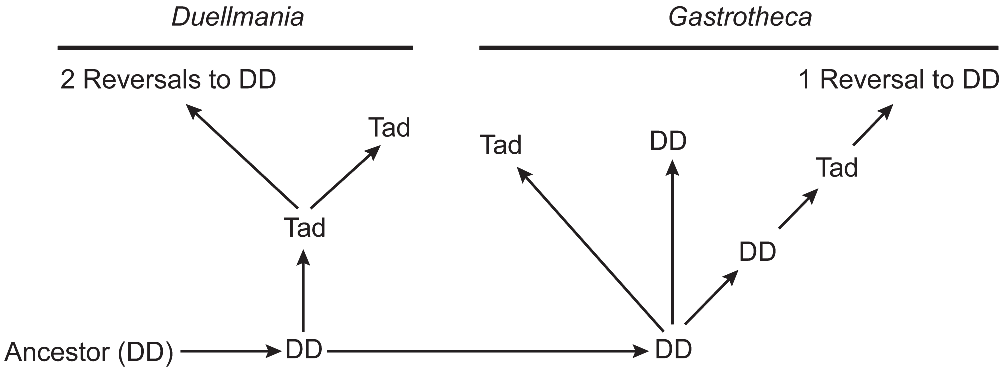


Fig. 3.2 Evolutionary trends in reproductive modes in the Andean subgenera *Duellmania* (two clades) and *Gastrotheca* (three clades). DD = direct development, Tad = tadpole.

as tadpoles occurs only in species of the subgenera *Duellmania* and *Gastrotheca* found at elevations mostly above 2000 m in the Andes. Reversal to direct development has occurred twice in subgenus *Duellmania* and perhaps as many as three times in the subgenus *Gastrotheca*, whereas the evolution of tadpole production may have occurred two or more times in these Andean frogs. This transmutable mode of life history demands further study, both phylogenetically and embryologically (chapter 7).

In the present analysis of molecular data, the basal taxa are grouped into four subgenera, with *Eotheca* being the basal subgenus. In one Bayesian analysis, *Amphignathodon* was basal. Limited sequence data may be responsible for some placements in the tree. *Gastrotheca ovifera* is an enigma. Wiens et al. (2007) used only one gene (16S) from *G. ovifera* in their analysis. In the phylogeny presented here, a second gene (ND1) was added. In the results of both analyses, *G. ovifera* is a single taxon not closely related to any of the subgenera (but see chapter 4). Although taxon sampling of *Gastrotheca* is reasonably good (80% of the species), many more genes need to be sequenced. Moreover, many of the sequences were obtained from tissues that I collected in the 1970s; obviously, fresh tissues are desirable. Only the one problematic tissue sample of *G. ovifera* exists. Because this species may be extinct (Valera-Leal et al., 2011), additional sampling may not be possible, given our technological constraints.

An analysis of multiple character states of 43 cranial characters proved to be of limited and uneven success in solving relationships, a result also proclaimed by Mendelson et al. (2000). The four large species of *Eotheca* are clearly defined by osteological synapomorphies; both the sister-group status of *Gastrotheca walkeri* and *Stefania* and the placement of *Gastrotheca* (*Amphignathodon*) *bufona* in the subgenus *Gastrotheca* are confirmed. External morphological characters were of limited significance in the phylogenetic analyses. Proportionally short hind limbs differentiate the subgenera *Duellmania* and *Gastrotheca* from the long-legged *Amphignathodon*. Most species in the latter subgenus are adorned with supraciliary processes and calcars on the heels; these characters are absent in most other *Gastrotheca*. Coloration and color patterns are useful in distinguishing some species, but these characters are useless in phylogenetic analyses because of interspecific variation and ontogenetic changes.

An analysis of genomic data and osteological characters was far more successful; there was concordance in the two datasets among the basal subgenera, but there were exceptions (chapter 4). Furthermore, the combined datasets recognized the two Andean subgenera (*Duellmania* and *Gastrotheca*), although there were some discrepancies in comparison with the genomic tree. These are discussed in detail in chapter 4.

Classification

Formal classification and its associated nomenclature should reflect the phylogenetic relationships of monophyletic genera, of which there are six in the family Hemiphractidae. Since Fitzinger's (1843) proposal of the generic name *Gastrotheca*, 15 generic-level names (exclusive of the subgenera named herein) have been proposed for species of hemiphractid frogs (Table 3.1). Some of these were replacement names for earlier names that were preoccupied; others were substitute names. Günther (1859:115) proposed the generic name *Nototrema* as a substitute name for *Gastrotheca*. His generic name was used throughout the later part of the nineteenth and early part of the twentieth centuries.

Table 3.1 Alphabetical synonymy of genus-group names in the Hemiphractinae

Generic name (type species) author, date	Present name
Amphignathodon (*Amphignathodon guentheri*) Boulenger, 1882	*Gastrotheca*
Cerathyla (*Cerathyla bubalus*) Jiménez de la Espada, 1871	*Hemiphractus*
Coelonotus (*Coelonotus fissilis*) Miranda-Ribeiro, 1920	*Fritziana*
Cryptobatrachus (*Cryptobatrachus boulengeri*) Ruthven, 1916	*Cryptobatrachus*
Duellmania (*Hyla argenteovirens*) Dubois, 1987	*Gastrotheca*
Flectonotus (*Nototrema pygmaeum*) Miranda-Ribeiro, 1926	*Flectonotus*
Fritzia (*Hyla goeldii*) Miranda-Ribeiro, 1920	*Fritziana*
Fritziana (*Hyla goeldii*) Mello-Leitão, 1937	*Fritziana*
Gastrotheca (*Hyla marsupiata*) Fitzinger, 1843	*Gastrotheca*
Hemiphractus (*Hemiphractus spixii*) Wagler, 1828	*Hemiphractus*
Notodelphys (*Notodelphys ovifera*) Lichtenstein and Weinland, 1854	*Gastrotheca*
Nototheca (*Coelonotus fissilis*) Bokermann, 1950	*Fritziana*
Nototrema (*Hyla marsupiata*) Günther, 1859	*Gastrotheca*
Opisthodelphys (*Notodelphys ovifera*) Günther, 1859	*Gastrotheca*
Stefania (*Hyla evansi*) Rivero, 1968	*Stefania*

Other generic names were based on species having different morphological characters. Jiménez de la Espada (1871) placed small species of *Hemiphractus* in a different genus, *Cerathyla*. This name was synonymized by Noble (1926), a decision supported by the present genetic data. Boulenger (1882) was astonished to find a frog with teeth on the dentary, a feature known only in this one species today. He created a new genus for it, *Amphignathodon*, which, despite this taxon's unique condition, was shown to be a *Gastrotheca* by Duellman et al. (1988).

Thus the family Hemiphractidae contains six genera: *Cryptobatrachus* (6 species), *Flectonotus* (2 species), *Fritziana* (4 species), *Gastrotheca* (69 species), *Hemiphractus* (6 species), and *Stefania* (19 species). *Gastrotheca* is treated in detail with species accounts in chapters 10–12. The nomenclature of the family is given in chapter 9, and the family and other remaining genera are treated solely at the generic level in chapter 9. Junior synonyms of one species of *Cryptobatrachus* and four species of *Hemiphractus* are given in Frost (2013). Ninety-four specific and subspecific names have

Table 3.2 Trivial names and their present assignment in *Gastrotheca*

Trivial name (original combination) author, date	Subgenus	Present name
abdita (*Gastrotheca*) Duellman, 1987b	*Gastrotheca*	*G. abdita*
aguaruna (*Gastrotheca*) Duellman, Barley, and Venegas, 2013	*Gastrotheca*	*G. aguaruna*
albolineata (*Hyla*) Lutz and Lutz, 1939	*Australotheca*	*G. albolineata*
andaquiensis (*Gastrotheca*) Ruíz and Hernández, 1976	*Amphignathodon*	*G. andaquiensis*
angustifrons (*Nototrema*) Boulenger, 1898	*Amphignathodon*	*G. angustifrons*
antomia (*Gastrotheca*) Ruíz, Ardilla, Lynch, and Restrepo, 1997	*Amphignathodon*	*G. antomia*
aratia (*Gastrotheca*) Duellman, Barley, and Venegas, 2013	*Gastrotheca*	*G. aratia*
argenteovirens (*Hyla*) Boettger, 1892	*Duellmania*	*G. argenteovirens*
atympana (*Gastrotheca*) Duellman, Lehr, et al., 2004	*Gastrotheca*	*G. atympana*
aureomaculata (*Gastrotheca*) Cochran and Goin, 1970	*Duellmania*	*G. aureomaculata*
bifasciata (*Gastrotheca marsupiata*) Vellard, 1957	*Gastrotheca*	*G. griswoldi*
binghami (*Eleutherodactylus*) Stejneger, 1913	*Gastrotheca*	*G. marsupiata*
bolivianum (*Nototrema*) Steindachner, 1892	*Gastrotheca*	*G. marsupiata*
bufona (*Gastrotheca*) Cochran and Goin, 1970	*Amphignathodon*	*G. bufona*
caeruleomaculatus (*Hylodes*) Werner, 1899	*Gastrotheca*	*G. caeruleomaculata*
capitocarinata (*Hyla*) Andersson, 1945	*Amphignathodon*	*G. longipes*
carinaceps (*Gastrotheca*) Duellman, Trueb, and Lehr, 2006	*Gastrotheca*	*G. carinaceps*
cavia (*Gastrotheca*) Duellman, 1974a	*Duellmania*	*G. riobambae*
ceratophrys (*Hyla*) Stejneger, 1911	*Amphignathodon*	*G. cornuta*
christiani (*Gastrotheca*) Laurent, 1967	*Gastrotheca*	*G. christiani*
chrysosticta (*Gastrotheca*) Laurent, 1976	*Gastrotheca*	*G. chrysosticta*
cornutum (*Nototrema*) Boulenger, 1898	*Amphignathodon*	*G. cornuta*
cuzcanus (*Chorophilus*) Cope, 1877	*Gastrotheca*	*G. marsupiata*
dendronastes (*Gastrotheca*) Duellman, 1983b	*Amphignathodon*	*G. dendronastes*
descampsi (*Gastrotheca nicefori*) Lutz and Ruíz, 1977	*Duellmania*	*G. nicefori*
dissimilis (*Gastrotheca peruana*) Vellard, 1957	*Gastrotheca*	*G. peruana*

continued

Table 3.2 continued

Trivial name (original combination) author, date	Subgenus	Present name
dorsigera (*Notodelphys*) Schlegel, 1858	*Opisthodelphys*	*G. ovifera*
dunni (*Gastrotheca argenteovirens*) Lutz, 1977	*Duellmania*	*G. dunni*
dysprosita Duellman, 2013	*Duellmania*	*G. dysprosita*
ecuatoriensis (*Gastrotheca marsupiata*) Vellard, 1957	*Duellmania*	*G. riobambae*
ernestoi (*Gastrotheca*) Miranda-Ribeiro, 1920	*Australotheca*	*G. ernestoi*
espeletia (*Gastrotheca*) Duellman and Hillis, 1987	*Duellmania*	*G. espeletia*
excubitor (*Gastrotheca*) Duellman and Fritts, 1972	*Gastrotheca*	*G. excubitor*
fissipes (*Nototrema*) Boulenger, 1888	*Eotheca*	*G. fissipes*
flamma (*Gastrotheca*) Juncá and Nunes, 2008	*Australotheca*	*G. flamma*
footei (*Eleutherodactylus*) Stejneger, 1913	*Gastrotheca*	*G. marsupiata*
fulvorufa (*Nototrema*) Andersson, 1911	*Australotheca*	*G. fulvorufa*
galeata (*Gastrotheca*) Trueb and Duellman, 1978	*Edaphotheca*	*G. galeata*
gracilis (*Gastrotheca*) Laurent, 1969b	*Gastrotheca*	*G. gracilis*
griswoldi (*Gastrotheca*) Shreve, 1941	*Gastrotheca*	*G. griswoldi*
guentheri (*Amphignathodon*) Boulenger, 1882	*Amphignatthodon*	*G. guentheri*
helenae (*Gastrotheca*) Dunn, 1944	*Amphignathodon*	*G. helenae*
humbertoi (*Gastrotheca*) Lutz, 1977	*Amphignathodon*	*G. andaquiensis*
juninensis (*Gastrotheca peruana*) Vellard, 1957	*Gastrotheca*	*G. peruana*
lateonota (*Gastrotheca*) Duellman and Trueb, 1988	*Duellmania*	*G. lateonota*
lauzuricae (*Gastrotheca*) De la Riva, 1992	*Gastrotheca*	*G. caeruleomaculata*
litonedis (*Gastrotheca*) Duellman and Hillis, 1987	*Duellmania*	*G. litonedis*
lojana (*Gastrotheca marsupiata*) Parker, 1932	*Duellmania*	*G. monticola*
longipes (*Nototrema*) Boulenger, 1882	*Duellmania*	*G. longipes*
marsupiata (*Hyla*) Duméril and Bibron, 1841	*Gastrotheca*	*G. marsupiata*
medemi (*Gastrotheca*) Cochran and Goin, 1970	*Duellmania*	*G. nicefori*
megacephala (*Gastrotheca*) Izecksohn et al., 2009	*Eotheca*	*G. megacephala*
mertensi (*Gastrotheca*) Cochran and Goin, 1970	*Duellmani*	*G. aureomaculata*
microdiscus (*Nototrema*) Andersson *in* Lönnberg et al., 1910	*Australotheca*	*G. microdiscus*
monticola (*Gastrotheca*) Barbour and Noble, 1920a	*Duellmania*	*G. monticola*
nebulanastes (*Gastrotheca*) Duellman et al., 2011	*Gastrotheca*	*G. nebulanastes*
nicefori (*Gastrotheca*) Gaige, 1933	*Duellmania*	*G. nicefori*
ochoai (*Gastrotheca*) Duellman and Fritts, 1972	*Gastrotheca*	*G. ochoai*
olivaceus (*Chorophilus*) Andersson, 1945	*Duellmania*	*G. riobambae*
ossilaginis (*Gastrotheca*) Duellman and Venegas, 2005	*Gastrotheca*	*G. ossilaginis*
orophylax (*Gastrotheca*) Duellman and Pyles, 1980	*Duellmania*	*G. orophylax*
ovifera (*Notodelphys*) Lichtenstein and Weinland, 1854	*Opisthodelphys*	*G. ovifera*
pacchamama (*Gastrotheca*) Duellman, 1987b	*Gastrotheca*	*G. pacchamama*
parkeri (*Hyla*) DeWitte, 1930a	*Australotheca*	*G. microdiscus*
parkeriana (*Hyla*) DeWitte, 1930b	*Australotheca*	*G. microdiscus*
peruanum (*Nototrema*) Boulenger, 1900	*Gastrotheca*	*G. peruana*
phalarosa (*Gastrotheca*) Duellman and Venegas, 2005	*Gastrotheca*	*G. phalarosa*
piperata (*Gastrotheca*) Duellman and Kóhler, 2005	*Gastrotheca*	*G. piperata*
plumbeum (*Nototrema*) Boulenger, 1882	*Duellmania*	*G. plumbea*
prasina (*Gastrotheca*) Teixeira, Vechio, et al., 2012	*Eotheca*	*G. prasina*
pseustes (*Gastrotheca*) Duellman and Hillis, 1987	*Gastrotheca*	*G. pseustes*
psychrophila (*Gastrotheca*) Duellman, 1974a	*Gastrotheca*	*G. psychrophila*
pulchra (*Gastrotheca*) Caramaschi and Rodrigues, 2007	*Australotheca*	*G. pulchra*
pusilla (*Hyla*) Melin, 1941	*Amphignathodon*	*G. weinlandii*
quitoe (*Hyla*) Fowler, 1913	*Duellmania*	*G. riobambae*
rebeccae (*Gastrotheca*) Duellman and Trueb, 1988	*Gastrotheca*	*G. rebeccae*
recava (*Gastrotheca*) Teixeira, Vechio, et al., 2012	*Eotheca*	*G. recava*
riobambae (*Hyla*) Fowler, 1913	*Duellmania*	*G. riobambae*
ruizi (*Gastrotheca*) Duellman and Burrowes, 1986	*Duellmania*	*G. ruizi*
splendens (*Hyla*) Schmidt, 1857	*Gastrotheca*	*G. splendens*
stictopleura (*Gastrotheca*) Duellman. Lehr, and Aguilar, 2001	*Gastrotheca*	*G. stictopleura*
testudineum (*Nototrema*) Jiménez de la Espada, 1871	*Gastrotheca*	*G. testudinea*
trachyceps (*Gastrotheca*) Duellman, 1987a	*Duellmani*	*G. trachyceps*

Table 3.2 continued

Trivial name (original combination) author, date	Subgenus	Present name
vellardi (*Gastrotheca bifasciata*) Laurent, 1969b	*Gastrotheca*	*G. marsupiata*
viridis (*Gastrotheca*) Lutz and Lutz, 1939	*Australotheca*	*G. ernestoi*
viviparum (*Nototrema*) Andersson, 1945	*Gastrotheca*	*G. testudinea*
vogli (*Hyla*) Müller, 1938	*Opisthodelphys*	*G. ovifera*
walkeri (*Gastrotheca*) Duellman, 1980	*Cryptotheca*	*G. walkeri*
weinlandii (*Nototrema*) Steindachner, 1892	*Amphignathodon*	*G. weinlandii*
williamsoni (*Gastrotheca*) Gaige, 1922	*Cryptotheca*	*G. williamsoni*
yacambuensis (*Gastrotheca*) Yústiz, 1978	*Duellmania*	*G. nicefori*
zeugocystis (*Gastrotheca*) Duellman, Lehr, et al., 2004	*Gastrotheca*	*G. zeugocystis*

been applied to the 69 recognized species of *Gastrotheca* (Table 3.2).

In the past decade or so, many phylogenetic analyses of molecular data have revealed the existence of well-supported clades, distinguishable or not by morphological characters. In some cases (e.g., Nicholson et al., 2012), a large genus with a well-known name has been fragmented into several genera. In other instances (e.g., Wake, 2012), distinct clades within large genera have been recognized as subgenera. In order to retain the well-known generic name *Gastrotheca*, I recognize eight subgenera within that genus. These are formally presented and defined in the taxonomic sections in chapters 10–12.

Vernacular Names

The original description of *Hyla marsupiata* (Duméril and Bibron, 1841) initiated the usage of the term marsupial frog, a name that has been applied to all members of the genus *Gastrotheca*. Some vernacular (common) names applied by persons familiar with the frogs are reasonable epithets, such as Cochran (1961) referring to the Brazilian species of *Flectonotus* (now *Fritziana*) as Egg-carrying Treefrogs. Most other so-called common names have been coined by authors with no first-hand knowledge of the organisms. Consequently, most of their common names have little or no meaning. For example, Frank and Ramus (1995) termed *Cryptobatrachus* Backpacking Treefrogs, a name equally applicable to *Stefania*, which they called Stefania, and *Hemiphractus*, which they and Ananjeva et al. (1988) referred to as Horned Treefrogs. I have avoided the use of such epithets, except for applying the term marsupial frog to members of the genus *Gastrotheca*.

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4

LINDA TRUEB

Osteology

The body plan of neobatrachian anurans frequently is cited as an exemplar of a design that combines efficient saltatorial locomotion with specialized modes of feeding, as described by Gans (1961, 1974) and Gans and Gorniak (1982a, 1982b). This functionality results from lengthened hind limbs and a modification of the tarsus. When the frog is perched or sitting, its trunk is flexed around the sacral joint of the vertebral column, which articulates with the pelvis. As the frog initiates a leap, the hind limbs unfold to propel the animal forward as the trunk straightens at the sacrum. Simultaneously, the short forelimbs are folded along the flanks of the body and the eyes are pulled into the orbits; thus the body assumes a fusiform shape that can be efficiently thrust forward as the frog leaps. As the apogee of the jump is achieved, the forelimbs rotate forward and the frog lands on its hands, with the force of landing being absorbed by the pectoral girdle.

Anuran osteological diversity was surveyed by Lynch (1973), Trueb (1973, 1993), and Duellman and Trueb (1986). The architectural plan underpinning saltatorial locomotion and distinguishing anurans from other tetrapods includes hind limbs that are much longer than the forelimbs and have an extra joint between the elongated proximal tarsal elements and the distal foot. The pelvic girdle is elongated, and the axial column is modified by a fusion of the postsacral vertebrae into the rod-like urostyle; the sacrum is expanded, and the vertebral column is shortened by an elimination of some presacral vertebrae (Pugener, 2002). The anuran skull is depressed, and the lower jaw usually lacks serrations, odontoids, and teeth. The short forelimbs have a reduced number of digits in the hand, with the first preaxial digit having been lost (Alberch and Gale, 1983). The pectoral girdle is either arciferal or firmisternal; both are adapted to absorb the shock of a frog's leaping and landing on its forelimbs, but in different ways (Emerson, 1983). In an arciferal girdle the midventral halves of the zonal girdle overlap one another and are united only by a slender bridge of cartilage anteriorly. In contrast, the zonal elements of a firmisternal girdle are solidly fused to one another midventrally, and usually there are elaborate pre- and postzonal midventral elements (Duellman and Trueb, 1986). The hyoid apparatus, which lies in the floor of the mouth above and anterior to the pectoral girdle, supports the tongue and its protrusion from the mouth, except in one lineage, the peculiar Pipidae. Given this unusual suite of specialized features, it commonly is assumed that there is little significant osteological variation in this lineage of some 6000 taxa.

Although the fundamental design of all anurans is the same, there indeed are significant differences in the structure of some osteological components. Thus, among basal archaeobatrachian taxa (e.g., Ascaphidae, Alytidae, Bombinatoridae, Discoglossidae, Rhinophrynidae, Pipidae, Pelobatidae, and Pelodytidae, with all other anurans being members of the more derived neobatrachians), the joints between the presacral vertebrae may be amphicoelous, opisthocoelous, or procoelous (Duellman and Trueb, 1986). All members of the neobatrachian clade have eight or fewer procoelous presacral vertebrae and lack free ribs; the transverse processes vary in length. The numbers of digits on the manus and pes are reduced in some taxa. The design of arciferal or firmisternal pectoral girdles can be strikingly different, and in some taxa parts of these girdles may be reduced or absent. The hyoid apparatus serves as a platform from which the tongue is catapulted from the mouth in all neobatrachians, except microhylids (Ritter and Nishikawa, 1995); in the latter family, the tongue seems to be protruded via a hydrostatic mechanism that is, in some ways, similar to the mechanism in Rhinophrynidae (Gans and Gorniak, 1982b; Trueb and Cannatella, 1982; Trueb and Gans, 1983).

The basic plan of the cranium includes paired olfactory capsules and a braincase composed of the sphenethmoid anteriorly and the prootic and exoccipitals posteriorly; the latter elements also form the otic capsules on either side of the posterior end of the braincase. The plectrum (stapes) may be complete or lack components; the tympanum may be present or absent. The skull table consists of paired nasals roofing the olfactory capsules anterior to the braincase, paired frontoparietals covering the dorsum of the braincase, and the dorsal surface of the sphenethmoid (if it is exposed). In some taxa the dorsal surface of the sphenethmoid is covered by an expansion of either, or both, of the nasals and frontoparietals. In most taxa, the bone is exposed; it either is smooth (i.e., not exostosed) or sculptured. If sculpturing is present, it is formed by membranous bone that fuses in various patterns to the underlying endochondral (i.e., cartilage-replacement) bone, and the dorsally exposed surface of such a compound bone is termed a dermal sphenethmoid (Trueb, 1966, 1970). The ventral surface of the skull usually has a pair of vomers that are dentate or edentate and support the olfactory capsules; the T-shaped parasphenoid bone underlies the otic capsules and the ventral surface of the braincase, bridging the gap between the prootic posteriorly and the sphenethmoid anteriorly. The upper jaw is composed of a pair of premaxillae at the end of the snout and the maxillae that form most of the upper jaw; the maxillae may be dentate or edentate. If the upper jaw articulates with the palatoquadrate/squamosal complex, a quadratojugal is present. The maxillary arcade is suspended from the skull via the squamosal and the palatoquadrate, and is variably braced by the pterygoid (always present) and the neopalatine (variably present). The lower jaw comprises the angulosplenial and dentary on either side of Meckel's cartilage and a pair of mentomeckelian bones anteriorly beneath the premaxilla. Teeth are absent from the dentary in all known species, except one.

Hemiphractid frogs do not deviate from the basic postcranial osteological plan of neobatrachians. Thus there are eight presacral procoelous vertebrae and an arciferal pectoral girdle that lacks any sign of reduction. The hand has four digits, and the foot, five; so far as is known, there is no reduction in the lengths of the digits. The hyobranchial skeleton has not been surveyed extensively, because most of the specimens available for examination were prepared as dry skeletons; based on previous work by Trewavas (1933), there seems to be nothing notably different in the hyoid of hemiphractids and most other neobatrachians.

The fundamental plan of the hemiphractid skull and its development (Lathrop, 1994; Haas, 1996a, 1996b, 2003) resembles that of other neobatrachians. The bones are neither reduced nor absent. In contrast to most other neobatrachian taxa, except some bufonids and casque-headed hylids, there is a clear evolutionary trajectory toward proliferation of the dermal bone by exostosis and casquing.

Allies of Marsupial Frogs

The basal hemiphractid lineages—*Cryptobatrachus* and *Flectonotus*—lack the dermal elaboration of the skull typical of most members of the family and, in most respects, resemble the outgroup taxa examined (i.e., *Ischnocnema*, *Pristimantis*, and *Telmatobius*). Members of both genera have well-constructed skulls with smooth non-ornamented dorsal roofing bones (Fig. 4.1). The nasals lack a medial articulation with one another, in contrast to nearly all the remaining hemiphractids; the

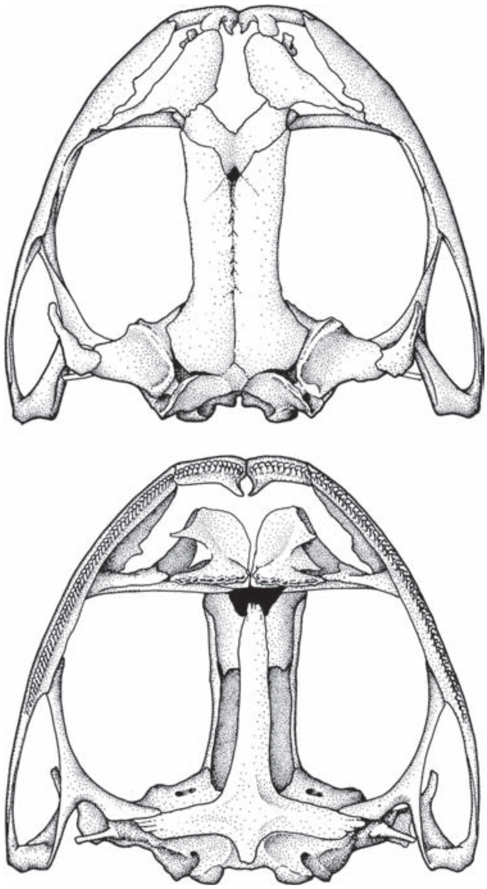

Fig. 4.1 *Cryptobatrachus conditus* (KU 169378, female) skull, shown in dorsal (*top*) and ventral (*bottom*) views. Note the broad medial separation of the nasals, and the incomplete articulation of the frontoparietals that exposes the frontoparietal fontanelle dorsally. The limited ossification of the sphenethmoid is evident ventrally; it results in an incomplete braincase in the region of the neopalatines and an extensive optic fenestra. The posterior position of the dentigerous processes of the vomers between the neopalatines is unusual. Drawings by L. Trueb.

nasals articulate with the frontoparietals in *Cryptobatrachus*, but not in *Flectonotus*. The frontoparietals have either a complete (*Flectonotus*) or partially complete (*Cryptobatrachus*) medial articulation and lack any peripheral elaboration laterally or posterolaterally; hence there is no differentiated carotid canal, and the canal is described as being open. The maxilla has an identifiable preorbital process and lacks a postorbital process; in this, as well as in other features of the upper jaw and its suspension, these taxa are more similar to the outgroup taxa (*Pristimantis*, *Telmatobius*) than the

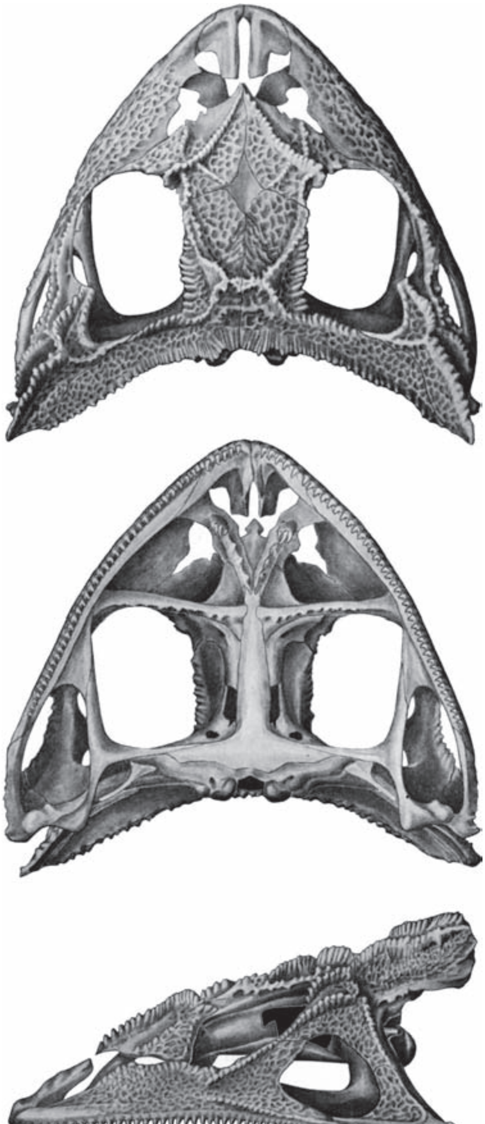

Fig. 4.2 *Hemiphractus bubalus* (KU 124140, female) skull, shown in dorsal (*top*), ventral (*middle*), and lateral (*bottom*) views. Note the extreme posterior deflection of the alary processes of the premaxillae; the presence of odontoids and serrations on the dentary, neopalatine, and vomer; and the disposition of the pterygoid with respect to the maxilla. *Hemiphractus* has a complete temporal arcade and a well-developed postorbital process on the maxilla that articulates with the massive, but short, zygomatic process of the squamosal. Drawings by L. Trueb.

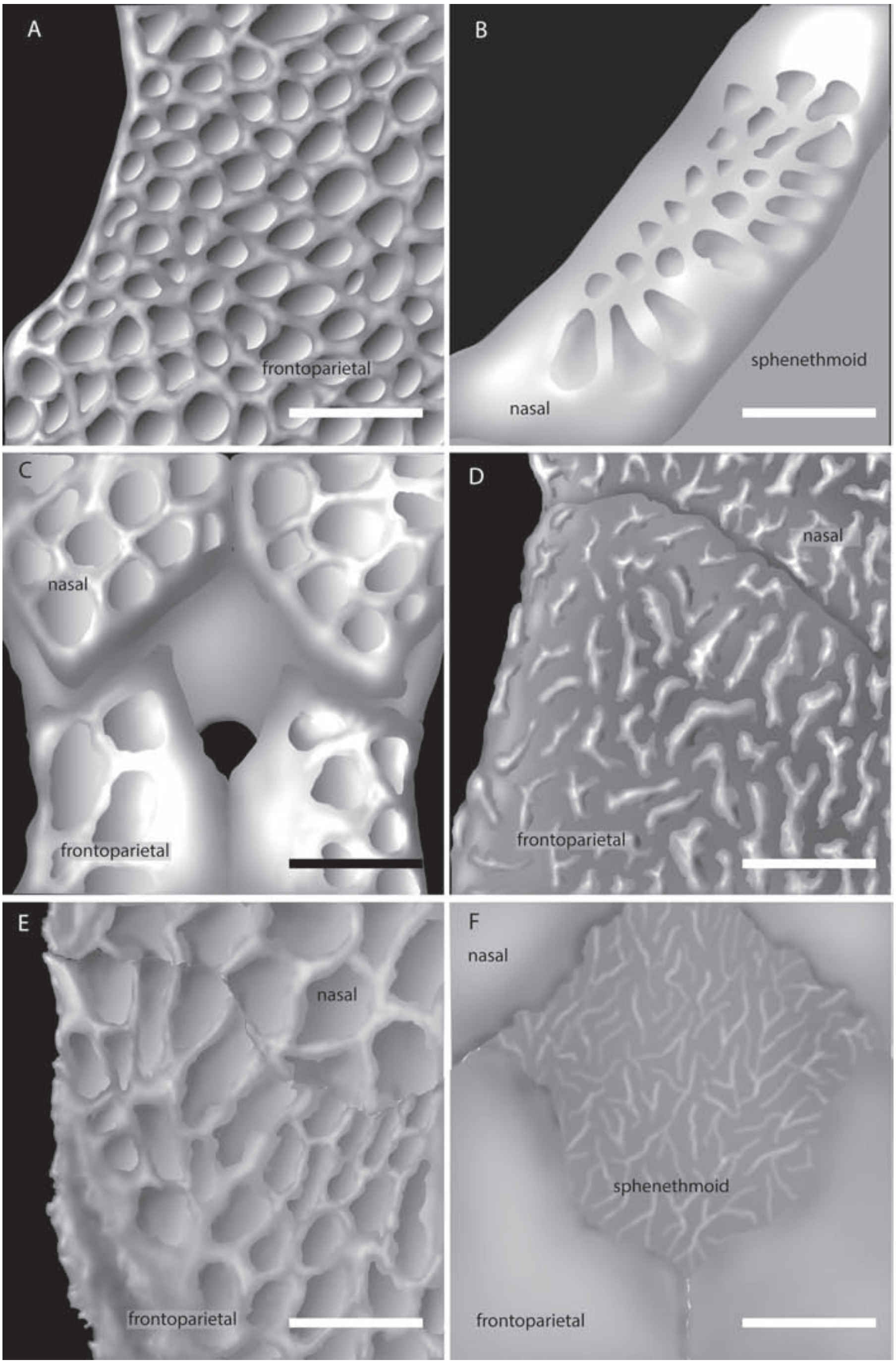
A
frontoparietal
B
sphenethmoid
nasal
C
nasal
frontoparietal
D
nasal
frontoparietal
E
nasal
frontoparietal
F
nasal
sphenethmoid
frontoparietal

Fig. 4.3 Dermal sculpturing in hemiphractid frogs. Each illustration (except B) shows a 3.5 × 3.5 mm sample from the midorbital region of the dorsal margin of the frontoparietal; in B, the bone depicted is the nasal. A: *Hemiphractus fasciatus* (KU 93510), with typical moderate-sized pit-and-ridge dermal sculpturing in which the margins of the pits are well defined. B: *Stefania scalae* (KU 181123), in which shallow irregularly shaped pits form only on the nasal bones. C: *Gastrotheca espeletia* (KU 178555), illustrating a coarse loose arrangement of shallow pits separated by low rounded ridges. D: *G. trachyceps* (KU 144124), in which the pattern of sculpturing is low irregular vermiform or ramus ridging. E: *G. cornuta* (KU 104361), with well-developed pit-and-ridge sculpturing that is irregular and characteristically has spicules along the external margins of sculpted bones, such as the orbital and occipital margins of the frontoparietal. F: *G. dendronastes* (KU 183832), showing the sphenethmoid that is smooth dorsally, but within which a vermiform pattern of internal ossification is visible. Scale bars represent 1 mm. Drawings by L. Trueb.

rest of the hemiphractids. The exceedingly short bony sphenethmoid (correlated with a large gap between the sphenethmoid and the prootic) is an apomorphy of *Cryptobatrachus*, as is the possession of broad dentigerous processes on the vomer that are transversely oriented between the neopalatines posterior to the chaoanae.

Members of the genus *Hemiphractus* are highly derived osteologically (Fig. 4.2; Trueb, 1974). The skull is broadly casqued but not co-ossified; none of the dermal bones are synostosed with another. All of the dermal bones are sculptured in a distinctive uniform pit-and-ridge pattern (Fig. 4.3); the sphenethmoid lacks a dorsal dermal component. The alary processes of the premaxillae are deflected posteriorly at an angle of approximately 60°; thus the rostrum and snout are markedly more depressed in lateral view than those of most anurans. The temporal arcade is complete, and the carotid canal is closed. Instead of pedicellate bicuspid teeth, *Hemiphractus* has recurved fang-like teeth on the maxilla and the premaxilla. Vomerine dentition is absent, but fang-like odontoids are present on these bones, as well as on the neopalatines. The dentary bears tooth-like serrations along its length and a pair of enlarged odontoids anteriorly. The preorbital process of the maxilla is expanded dorsomedially along the inner surface of the ventrolateral part of the nasal; the process is flange-like and articulates with the lateral end of the neopalatine. The squamosal, the quadratojugal, and the maxilla are expanded to enclose the postorbital temporal area laterally. In contrast to other casqued hemiphractids, the major part of the posterior margin of the orbit is composed of enormously expanded postorbital process of the maxilla, which articulates dorsolaterally with the zygomatic ramus of the squamosal. *Hemiphractus* is further distinguished from its sister clades by having long (i.e., wide) transverse processes on the vertebrae and prominent vertebral spines dorsally.

Hemiphractus obviously is a highly derived genus osteologically, but its sister taxa, *Fritziana* and *Stefania*, are not. Like *Hemiphractus*, they lack co-ossification. Although the skulls of *Fritziana* and *Stefania* are not casqued or heavily exostosed, there are nascent indications of dermal sculpturing. In *Fritziana*, internal ossification of the sphenethmoid forms a distinct vermiform pattern, although the dorsal surface is smooth. *Stefania* has pits in the nasal bones (Figs. 4.3B and 4.4), but the skull is otherwise devoid of ornamentation. The frontoparietals have a complete medial articulation in both genera. Both lack a supraorbital flange and posterior/posterolateral elaboration of the frontoparietals; hence a carotid canal is either absent or open. The nasals lack a medial articulation in *Fritziana*, but the articulation is complete or partial in *Stefania*. *Fritziana* has a broad articulation between the ventrolateral margin of the nasal and the maxilla, in contrast to *Stefania*. The neopalatine is simple and unornamented in *Fritziana*, whereas it bears an irregular ridge in *Stefania*. The zygomatic ramus of the squamosal is nearly complete to the maxilla in *Fritziana*, whereas in *Stefania* there is

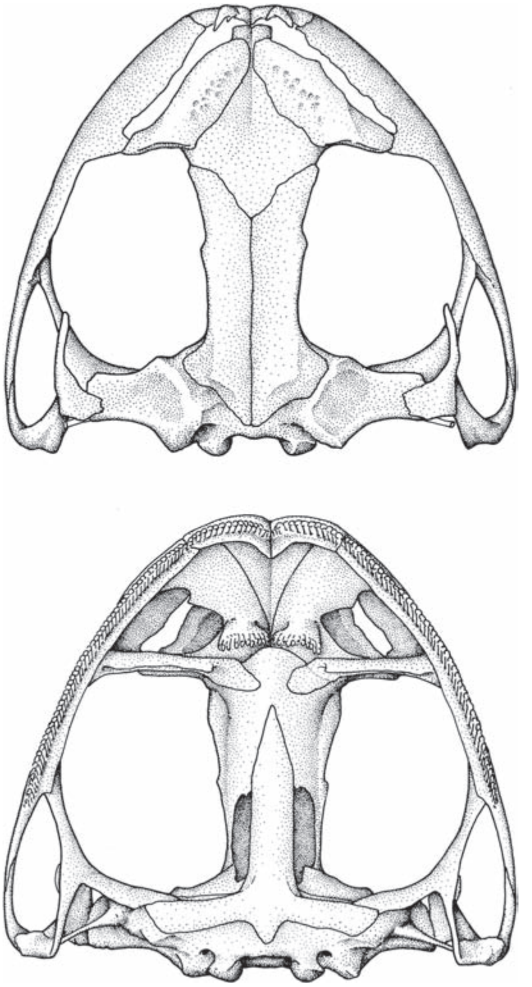

Fig. 4.4 *Stefania scalae* (KU 167671, female) skull, shown in dorsal (*top*) and ventral (*bottom*) views. Note that dermal sculpturing only occurs on the nasals, and that the frontoparietal has a narrow supraorbital flange. The sphenethmoid is ossified well posterior to the level of the midorbit. There is no canal for the carotid artery, which courses over the otic region between the anterior epiotic eminence and the posterolateral margin of the frontoparietal. The otic plate of the squamosal is poorly developed, overlapping only the posterolateral corner of the crista parotica. Drawings by L. Trueb.

a broad separation between the two bones. Arguably, *Stefania* is the closer relative to *Gastrotheca*, owing to the occurrence of exostosed skulls in all members of these two genera, except *G. bufona*, *longipes*, and the *griswoldi* + *pacchamama* clade. In many features, *Fritziana* and *Stefania* seem to be transitional between the *Cryptobatrachus* + *Flectonotus* clade and marsupial frogs of the genus *Gastrotheca*, with *Hemiphractus* being a curious and highly derived outlier.

Cranial Osteology of *Gastrotheca*

General Structure

Typically, species of *Gastrotheca* have robust skulls that are wider than long and widest at the level of the quadratojugal (Fig. 4.5). In lateral aspect, the skulls are boxy in appearance, owing to the massive temporal region, a flat skull table that extends nearly to the end of the snout, casqued dermal roofing bones, and the

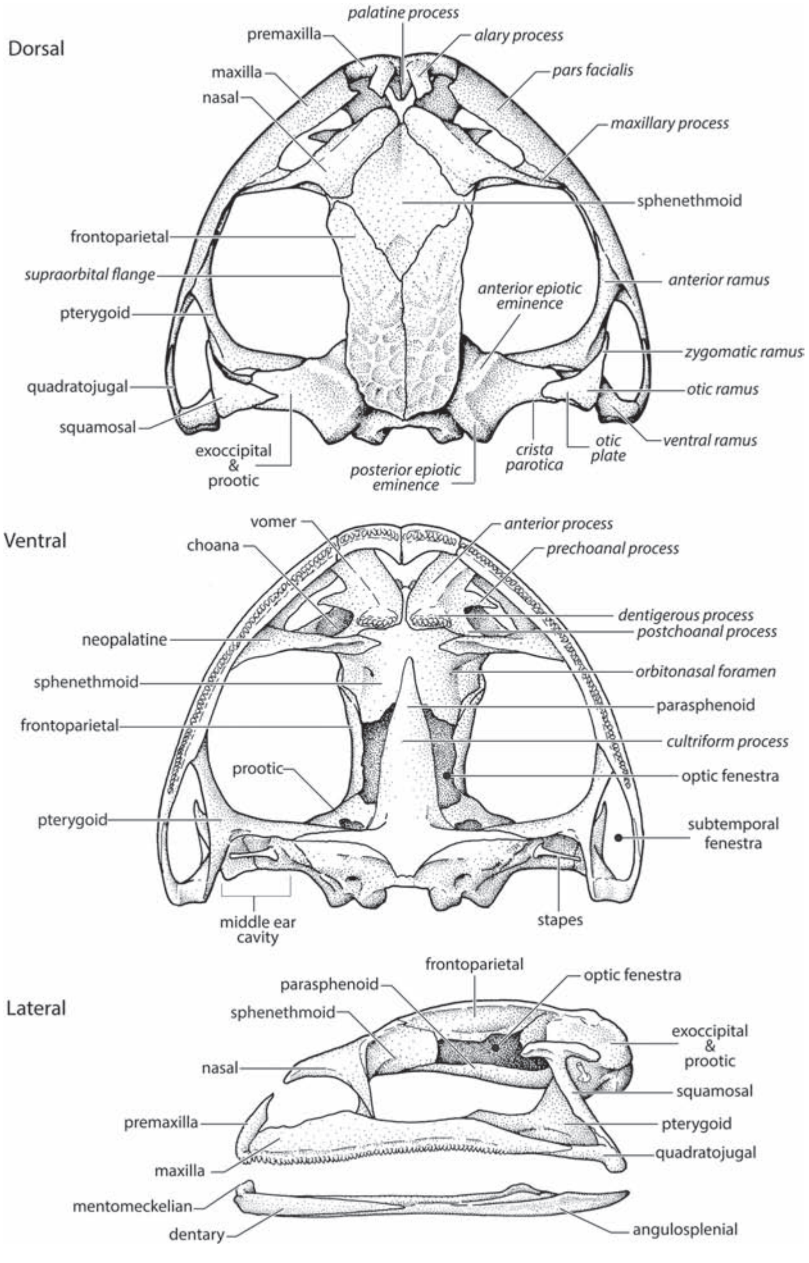
Dorsal
palatine process
premaxilla
alary process
maxilla
pars facialis
nasal
maxillary process
sphenethmoid
frontoparietal
supraorbital flange
anterior ramus
anterior epiotic eminence
pterygoid
zygomatic ramus
quadratojugal
otic ramus
squamosal
ventral ramus
exoccipital & prootic
posterior epiotic eminence
crista parotica
otic plate
Ventral
vomer
anterior process
choana
prechoanal process
dentigerous process
postchoanal process
neopalatine
orbitonasal foramen
sphenethmoid
parasphenoid
frontoparietal
cultriform process
prootic
optic fenestra
pterygoid
subtemporal fenestra
middle ear cavity
stapes
Lateral
frontoparietal
parasphenoid
optic fenestra
sphenethmoid
exoccipital & prootic
nasal
squamosal
premaxilla
pterygoid
quadratojugal
maxilla
mentomeckelian
dentary
angulosplenial

Fig. 4.5 *Gastrotheca walkeri* (KU 167851) skull in dorsal (*top*), ventral (*middle*), and lateral (*bottom*) views. Roman typeface is used to label the bones, whereas italics are used to designate a part of a bone (e.g., ramus, process, flange). Note that the exposed dorsal sphenethmoid is smooth, whereas the frontoparietals bear a low, reticulate pattern of sculpturing. The dermal sculpturing of the skull table is described as heterogeneous, because either the pattern varies from bone to bone or, as in this case, not all bones are sculpted. Drawings by L. Trueb.

massive alary processes of the premaxilla. The latter usually are nearly upright (i.e., minimal posterior deflection); hence the rostrum is high, and the end of the snout is blunt. The upper jaw is long, and the maxilla characteristically has a well-developed pars facialis, which contributes to the massive appearance of the skull. Dorsally, the skull is covered nearly completely in dermal bone composed of expanded nasals, frontoparietals, and squamosals. Ventrally, there are neopalatines and massive pterygoids. The ventral surface of the skull bears a well-developed parasphenoid, which occasionally is synostosed to the prootic and the exoccipital, and the large dentate vomers.

Among anurans, it is not unusual for the endocranium to be minimized in small or poorly ossified frogs or in taxa characterized by casquing and an elaboration of the dermal bones (e.g., *Triprion*). In *Gastrotheca*, the endocranium is substantial (Fig. 4.5). The braincase is broad and composed of a robust sphenethmoid, which is complete dorso- and ventromedially. Ossification of this element extends anterior to the plana antorbitale and underlies the posterior part of the vomer; in most taxa, the posteromedial margin of the choana is formed by the bony edge of the sphenethmoid. The orbitonasal foramen has a complete bony margin, but sphenethmoid ossification does not extend into the planum antorbitale; thus this part of the endocranium is cartilaginous. The posterior margin of the bony sphenethmoid usually lies near the midlength of the orbit or slightly posterior to it; the sphenethmoid is synostosed with the prootic in only two of the taxa examined, *G. bufona* and *G. megacephala*. The optic foramen lies in the cartilage between the sphenethmoid and the prootic in all *Gastrotheca*. Both the prootic and the exoccipital are extensively ossified. Ventrally, these bones may be synostosed with the underlying parasphenoid; dorsally, the prootic frequently is synostosed with the frontoparietal in the region of the epiotic eminences (see the description of the carotid canal below). The exoccipitals are complete and fused medially in their dorsal and ventral aspects.

All *Gastrotheca*, except one, have tympanic annuli and well-developed otic capsules composed of the exoccipital and the prootic; *G. atympana* lacks a tympanum but has a complete middle ear. The middle ear, marked by the crista parotica of the prootic, is wide, in keeping with the transverse breadth of the skull in the temporal region (Fig. 4.6). All species have a complete plectral apparatus, composed of a partes interna plectri (footplate), media plectri (stylus), and externa plectri (cartilaginous expanded distal end of the stylus). In most of the taxa examined, the stylus extends dorsolaterally from the fenestra ovalis toward the tympanum, but this orientation varies. The stylus is lateral in a few species (e.g., *G. andaquiensis*, *recava*, *ruizi*), ventrolateral in *G. antomia* and *G. aureomaculata*, and posterolateral in *G. angustifrons*. The configuration of the footplate (pars interna) of the plectrum in its posterior aspect varies. In most species the dorsal part is equal to or 1.5 times greater than the ventral portion. But in other species, the dorsal part is either 2–3 times broader than the ventral portion (e.g., *G. espeletia*, *griswoldi*, *helenae*, *monticola*, *pseustes*) or more than 3 times broader (e.g., *G. antomia*, *bufona*, *dunni*, *galeata*, *lateonota*, *marsupiata*, *weinlandii*).

Surface Configuration of Dermal Bones of the Skull Table

The maxilla, the squamosal, and elements of the dermal skull table of nearly all species of *Gastrotheca* are exostosed, sculpted in various patterns, and partially co-ossified, such that the overlying skin is completely or partially adherent to the adjacent bones below. This hyperossification is ubiquitous among the largest taxa (e.g., *G. antomia*) and least developed or (rarely) absent in the smallest (e.g., *G. ochoai*).

Three features of exostosis vary: (1) its distribution (i.e., the bones on which it occurs), (2) the nature of the pattern, and (3) the homogeneity of the pattern. The distribution of exostosis may be minimal (on the nasals and perhaps the frontoparietals), moderate (on the nasals, the frontoparietals, and the dorsal head of squamosals), or extensive (on the nasals, the frontoparietals, the entire squamosals, and the maxillae), depending on the species. Exostosis of the portion of the sphenethmoid exposed dorsally ranges from none to heavily exostosed and synostotically fused with the adjacent nasals and/or frontoparietals. Exostosis of the sphenethmoid is associated with co-ossification of the overlying skin. The membranous bone forms in the dermis; through a process of bone reconstruction as the frog matures, the dermal bone is incorporated structurally with the underlying endochondral (Trueb, 1966, 1970). In the case of co-ossified dermal bones, the union of the skin with the bone is simply accomplished by a fusion of bone formed in the membranous connective tissue with the deeper endochondral bone. These differences in formation may explain why, in some heavily exostosed and casqued *Gastrotheca*, the dorsally exposed sphenethmoid is not exostosed (i.e., smooth) and typically bears an internal vermiform

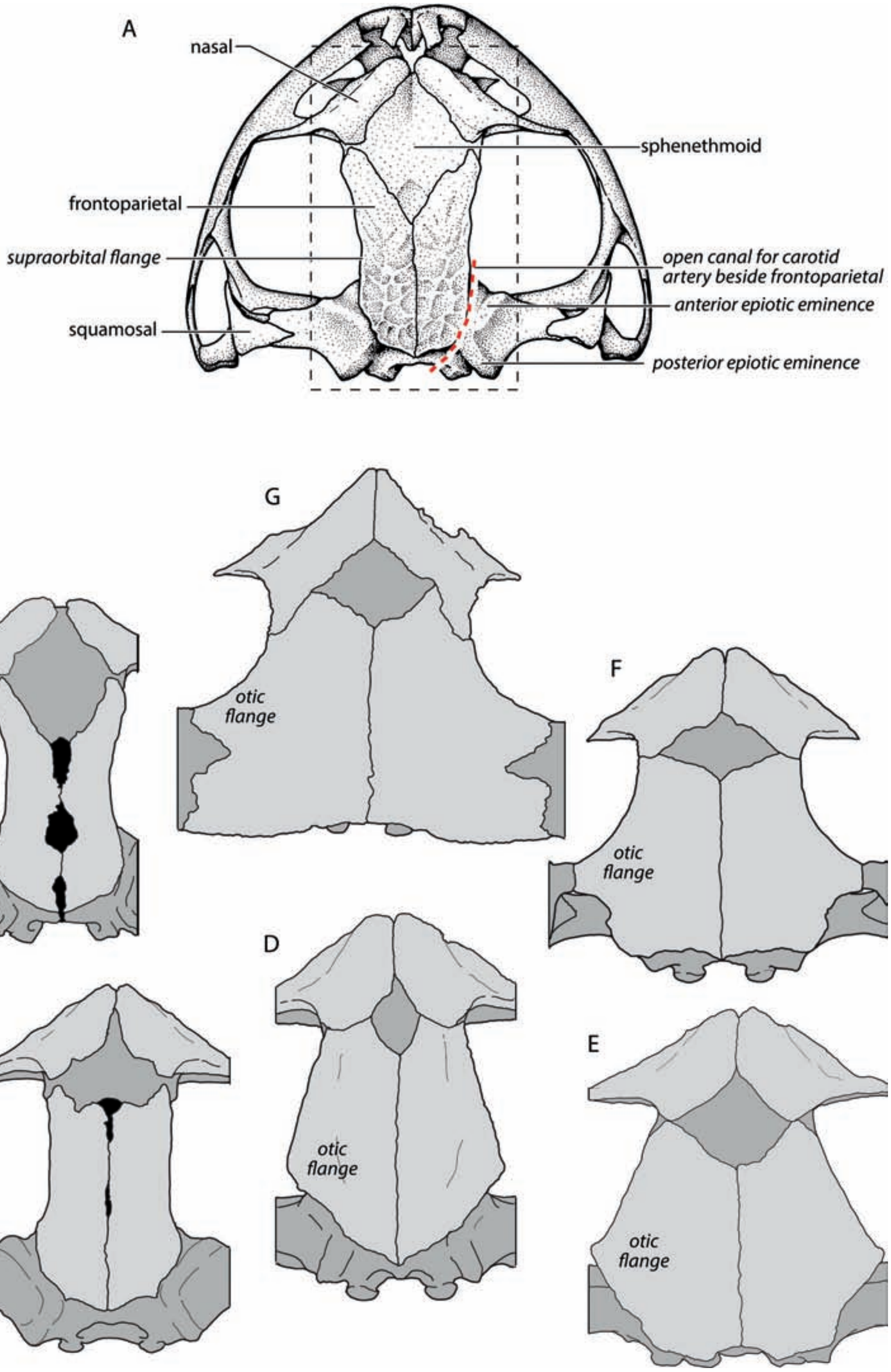
A
nasal
sphenethmoid
frontoparietal
supraorbital flange
open canal for carotid artery beside frontoparietal
anterior epiotic eminence
squamosal
posterior epiotic eminence
G
otic flange
B
F
otic flange
D
otic flange
C
E
otic flange

Fig. 4.6 Diversity of the skull table structure in *Gastrotheca*. A: *G. walkeri*, with the dashed rectangle indicating the area of the skull shown in figures B–G; roman typeface is used to label the bones, whereas italics are used to designate a part of a bone (e.g., flange). B: *G. andaquiensis*. C: *G. ochoai*. D: *G. helenae*. E: *G. testudinea*. F: *G. megacephala*. G: *G. monticola*. The dashed red line in A represents the course of the occipital artery from the occiput to the orbital cavity. Note the variation in the size of the frontoparietal and its relationships to the surrounding bones and the epiotic eminences. It has little lateral and posterolateral development in A–C; bears a moderately wide to wide supraorbital flange and otic flange in D and E; and is complete to the squamosal, forming a complete temporal arcade, in F and G. Variation in the relationship between the frontoparietal and nasal (and the resulting exposure of the sphenethmoid) is also evident in these figures. The figures are not drawn to the same scale. Drawings by L. Trueb.

pattern of ossification that indicates ossification of the cartilage-replacement bone. Unlike some other casqued co-ossified frogs, the sphenethmoid is always exposed in *Gastrotheca* and never covered by an expansion of the adjacent dermal bones.

Dermal sculpturing formed by exostosis can be classified loosely into topological types (Fig. 4.3). The presumed primitive states (based on developmental evidence) are the presence of low surface relief in a loose vermiform or ramus pattern, or the occurrence of superficial pits in the bone without the obvious development of ridges between them. Moderate to heavy sculpturing occurs in taxa with pit-and-ridge exostosis, of which there seem to be three different kinds. Most *Gastrotheca* have a semicoarse pattern of smooth ridges that separate moderate-sized shallow pits (i.e., pits moderate in size relative to the size of the frog's head); others have a coarse pattern of smooth ridges separating large shallow pits. The third type is a fine pattern characterized by extremely small pits (relative to the size of the frog) separated by sharp ridges that terminate variously with knobs or spicules. The pattern of dermal sculpturing across the skull table can be heterogeneous or homogeneous.

Casquing

Hyperossification also is manifested by casquing (i.e., marginal or peripheral expansion of the dermal bones) that usually is best developed in larger *Gastrotheca* (e.g., *G. megacephala*) and poorly developed or absent in small species (e.g., *G. ochoai*). Unlike some other casque-headed anurans (e.g., *Aparasphenodon*, *Corythomantis*, and *Triprion*), casquing does not involve the maxillary arcade in *Gastrotheca*. Instead, it is associated with hyperossification of the bones of the skull table: the nasals, the frontoparietals, and the squamosals (Fig. 4.7A–F). The nasals are expanded in most *Gastrotheca*, such that the contralateral bones have a complete medial articulation (but not in *G. plumbea*) and extend anteriorly over the rostrum to roof the olfactory capsule nearly completely, posterior to the premaxillae at the end of the snout. The nasal extends ventrolaterally to cover the side of the olfactory capsule; it articulates with the high pars facialis of the maxilla, forming a bony anterior orbital margin. The articulation between these elements occupies from 25% to more than 75% of the length of the rostrum from the orbit to the end of the snout; thus the lateral aspect of the olfactory capsule is well protected. Dorsally, the nasals typically overlap the anterior margin of the sphenethmoid and extend posteriorly along the dorsal margin of the orbit to articulate with the edges of the frontoparietals (Fig. 4.6). This articulation may be relatively narrow and limited to the anterolateral part of the frontoparietal (e.g., *G. longipes*) or broad (e.g., *G. helenae*); the extent of the articulation between the nasals and the frontoparietals determines the size of the exposed sphenethmoid. Depending on the amount of exostosis, the nasals may be synostotically united to one another and to the sphenethmoid; so far as is known, the nasals and the frontoparietals never are synostotically united to one another.

The frontoparietals in *Gastrotheca* (e.g., *G. testudinea*) usually have a complete medial articulation with one another, extending from the sphenethmoid posteriorly to the occiput in the region of the foramen magnum (Fig. 4.6). Nonetheless, there are exceptions (e.g., *G. andaquiensis*, *angustifrons*, *griswoldi*, *ochoai*, *pacchamama*), and a partial separation of the frontoparietals seems to bear no correlation with the size of the frog. Casquing of the frontoparietal is marked by a progressive marginal expansion: (1) the absence of a supraorbital flange or the presence of a narrow flange that is scarcely evident (e.g., *G. espeletia*, *excubitor*, and *marsupiata*); (2) a distinct and moderately developed flange (e.g., *G. andaquiensis*, *aureomaculata*, *riobambae*); and (3) a wide supraorbital flange (e.g., *G. fulvorufa* and *G. guentheri*).

In taxa with a supraorbital flange, the posterolateral margin of the frontoparietal either lies adjacent to the margin of the anterior epiotic eminence (e.g., *G. griswoldi*) or overlaps the anterior and the posterior epiotic eminences to varying degrees (e.g., *G. argenteovirens*, *dendronastes*, *marsupiata*, *monticola*; Fig. 4.6). The relationship of the posterolateral part of the frontoparietal flange to the underlying epiotic eminences of the otic capsule determines the condition of the carotid canal, which traverses the surface of the otic capsule medially, adjacent to the epiotic eminences, to emerge in the posterodorsal region of the orbit (Fig. 4.5). If there is no fusion between the ventral surface of the frontoparietal and the dorsal surface of the epiotic eminences, the canal is described as being open. Fusion of the frontoparietal with the corner of the epiotic eminences produces a partially closed carotid canal, whereas fusion with both the anterior and the posterior epiotic eminences results in an enclosed carotid canal. In most *Gastrotheca*, the carotid vessel courses caudad from a foramen (opening) on the occiput medial to the posterior epiotic eminence, but in a few taxa (e.g., *G. argenteovirens* and *G. plumbea*) there is a dorsal opening in the frontoparietal over the carotid canal that may be associated with it.

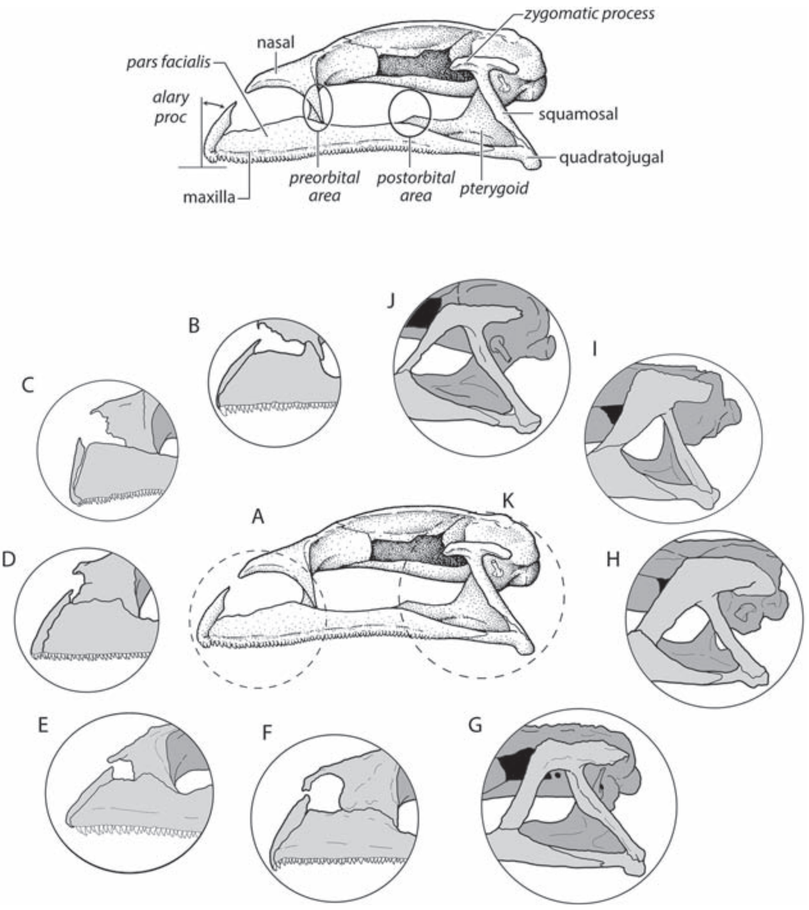

Fig. 4.7 Diversity of snouts and the suspensory apparatus in *Gastrotheca*. Roman typeface is used to label the bones, whereas italics are used to designate a part of a bone or the skull (e.g., process, area). A, K, and the upper labeled figure: *G. walkeri*, with dashed circles indicating areas of the skull shown in B–J. In the upper figure, note the angle of deflection of the alary process of the premaxilla, along with the pre- and postorbital areas of the skull. B: *G. andaquiensis*. C: *G. helenae*. D: *G. testudinea*. E: *G. ruizi*. F: *G. cornuta*. G: *G. cornuta*. H: *G. testudinea*. I: *G. helenae*. J: *G. andaquiensis*. Note the relationship of the pars facialis of the maxilla and the lateral margin of the nasal, and the nature of the articulation between the postorbital process of the maxilla and the zygomatic ramus of the squamosal. The figures are not drawn to the same scale. Drawings by L. Trueb.

Gastrotheca having moderate to wide supraorbital flanges may bear an otic flange, which is an expansion of the posterolateral frontoparietal at the posterior margin of the orbit (Fig. 4.6). In its least-developed condition, the flange is simply a triangular expansion of the frontoparietal (e.g., *G. aureomaculata*) over the otic region. A small otic flange (e.g., *G. helenae*) extends slightly laterally to the anterior epiotic eminence at the posteromedial margin of the orbit, whereas in species with a better-developed flange (e.g., *G. riobambae*), the flange covers the epiotic eminence and forms about half of the posterior margin of the orbit, but it remains widely separated from the head of the squamosal. Articulation of the otic flange of the frontoparietal with the head of the squamosal results in a bridge of dermal bone spanning the width of the otic capsule, herein termed a complete temporal arcade. An incomplete (partial) articulation occurs if the frontoparietal is united with the head of the zygomatic ramus squamosal to form a complete bony posterior margin of the orbit (e.g., *G. monticola*); such a temporal arcade is narrow. The arcade widens (e.g., *G. lojana*) as the articulation between the squamosal and the frontoparietal lengthens posteriorly. A complete articulation between the frontoparietal and the zygomatic and otic heads of the squamosal results in a wide temporal arcade that completely covers the otic capsule and the posterior margin, which forms the occiput of the skull (e.g., *G. fissipes* and *G. galeata*).

As mentioned above, the head of the squamosal in some *Gastrotheca* is elaborated dorsally and medially, such that the bone participates in the formation of the temporal arcade and, thereby, the skull table. In these taxa, the dorsal crest of the squamosal is described as being wide. In those taxa that have narrow crests (e.g., *G. albolineata*), there is some dorsal elaboration of the head of the squamosal, but no medial expansion.

Maxillary Arcade

The maxillary arcade is complete and bears a full complement of pedicellate bicuspid teeth in all *Gastrotheca*. A well-developed quadratojugal is present but is variable in length. In most species it is broadly overlapped laterally by the maxilla, but *G. pacchamama* is an exception, having only a tenuous articulation between the maxilla and the quadratojugal.

The maxilla, although not casqued, has a well-developed pars facialis that may have dermal sculpturing in some species (e.g., *Gastrotheca cornuta*). The pars palatina of the maxilla typically is narrow and unremarkable in *Gastrotheca*; posteriorly, it may be elaborated into a distinct medial process either articulating with the anterior ramus of the pterygoid (e.g., *G. fissipes*) or not (e.g., *G. longipes*). Typically, the pars facialis bears a dorsal process—i.e., the postorbital process that articulates with the zygomatic ramus of the squamosal at the posterior margin of the orbit (Fig. 4.7G–K). The nature of this articulation varies and is described below in relation to the suspensory apparatus of the skull. Although the pars facialis does not have a distinct preorbital process that can be identified in lateral view in most *Gastrotheca*, it is firmly articulated with the maxillary process of the nasal to form a complete bony anterior margin to the orbit in all *Gastrotheca*. The length of the articulation between the dorsal edge of the pars facialis and the ventrolateral margin of the nasal anterior to the orbit varies from about 25% of the length of the rostrum (e.g., *G. trachyceps*) to more than 75% (e.g., *G. carinaceps*).

In *Gastrotheca* the premaxillae tend to be broad and bear robust alary processes that, in most species of this genus, are inclined posteriorly at approximately an 11°–30° angle, producing a snout that is high and blunt in lateral profile (Fig. 4.7). In a few taxa (e.g., *G. griswoldi* and *G. recava*) the processes are nearly vertical, whereas in others they are deflected posteriorly at angles greater than 30° (e.g., *G. galeata* and *G. ruizi*). Like the maxilla, the premaxilla has a relatively narrow pars palatina that is medially elaborated into a moderate-sized medial palatine process; this process is markedly longer and spinous in a few species (e.g., *G. aureomaculata* and *G. cornuta*).

Of note is a variation in the relationship of the premaxilla and maxilla in *Gastrotheca*. The partes dentalis of these elements form a juxtaposed articulation in most species, with the pars dentalis of the maxilla slightly overlapping the lateral end of the pars dentalis of the premaxilla, a condition typical of most anurans. In a few *Gastrotheca* (e.g., *G. andaquiensis*, *antomia*, *galeata*), the pars dentalis of the maxilla broadly overlaps the premaxilla, suggesting a symphysial arrangement of the maxilla over the premaxilla. In addition, the pars facialis of the maxilla of some species (e.g., *G. galeata* and *G. nicefori*) extends anteromedially to contact the lateral margin of the alary process of the premaxilla.

Suspensory Apparatus

For the present purposes, the suspensory apparatus is defined as comprising the squamosal, the pterygoid, and the maxilla. Some features of the maxilla and the squamosal have been described above. Of particular relevance here are the otic plate and zygomatic ramus of the squamosal, the postorbital process of the maxilla, and the anterior ramus of the pterygoid (Figs. 4.5–4.8). The configurations of these structures and their articular relationships with one another vary among species of *Gastrotheca*, but most members of the genus are characterized by a complex group of articulations that seems to be unique among anurans.

In *Gastrotheca*, as in nearly all anurans, the triradiate pterygoid forms a three-way brace between the anteroventral margin of the otic capsule, the medial surface of the palatoquadrate cartilage at the jaw articulation, and the lingual margin of the maxilla in the postorbital region. The squamosal and the palatoquadrate cartilage suspend the maxillary arcade from the dorsum of the skull. The palatoquadrate is attached to the margin of the crista parotica via the otic process; the head of the squamosal overlies the latter and usually has a plate-like extension (otic plate) over the distal dorsal surface of the crista. The zygomatic ramus extends anteroventrally from the head of the squamosal and typically has a ligamentous connection with the pars facialis of the maxilla at the posterior margin of the orbit; in some taxa, the zygomatic ramus of the squamosal articulates with the hyperossified maxilla and/or quadratojugal (e.g., *Hemiphractus*, casque-headed hylids, ceratophyines, *Bufo*).

Gastrotheca conforms to the pattern described above, but various modifications of the anterior ramus of the pterygoid, the postorbital process of the maxilla, and the squamosal result a complex and robust articulation among these three structures (Fig. 4.8). The squamosal is well developed and usually hyperossified in *Gastrotheca* (Figs. 4.6 and 4.7). A dorsal crest on the head of the squamosal is lacking in only a few species (e.g., *G. christiani*, *griswoldi*, *ochoai*, *pacchamama*, *walkeri*); in the other taxa, it is well developed and may articulate with the frontoparietal to form a complete temporal arcade. In contrast, the otic plate of most species is poorly developed as a narrow marginal plate along the dorsolateral margin of the crista parotica. In some taxa the plate is moderately wide—i.e., covering 30%–50% of the width of the crista (e.g., *G. angustifrons*, *carinaceps*, *fulvorufa*, *helenae*, *ovifera*, *walkeri*); in others it covers more than 60% of the width of the crista (e.g., *G. albolineata*, *andaquiensis*, *bufona*, *guentheri*).

The zygomatic ramus of the squamosal lacks a bony articulation with the maxilla in only a few taxa (e.g., *G. chrysosticta*, *griswoldi*, *ochoai*, *walkeri*). The ramus is narrow in some (e.g., *G. albolineata*, *andaquiensis*, *angustifrons*, *cornuta*, *excubitor*, *piperata*). In most *Gastrotheca*, hyperossification has resulted in a zygomatic ramus that is broad in its lateral aspect; the ramus articulates with the postorbital process of the maxilla via a broad horizontal or diagonal articulation. In species in which the ramus does not reach the maxilla or in which it is narrow, the postorbital process may be absent or scarcely evident (e.g., *G. angustifrons*, *gracilis*, *griswoldi*, *ochoai*, *walkeri*); it also may not be obvious in many taxa with an expanded zygomatic ramus (e.g., *G. galeata*, *ovifera*, *zeugocystis*). Hyperossification of the ramus usually is associated with a well-developed postorbital maxillary process, and the articulation between these structures is either diagonal or in the horizontal plane of the skull.

In most anurans the anterior ramus of the pterygoid articulates with the lingual edge of the pars dentalis / pars palatina of the maxilla and, occasionally, with the maxilla via a pterygoid process elaborated at the posterior end of the pars palatina. A few *Gastrotheca* (e.g., *G. antomia*, *chrysosticta*, *galeata*, *griswoldi*, *guentheri*, *ochoai*, *recava*, *walkeri*) conform to this model and lack a dorsal process on the anterior ramus of the pterygoid that characterizes other members of the genus.

When present, the dorsal process of the anterior ramus of the pterygoid varies from broad and low (e.g.,

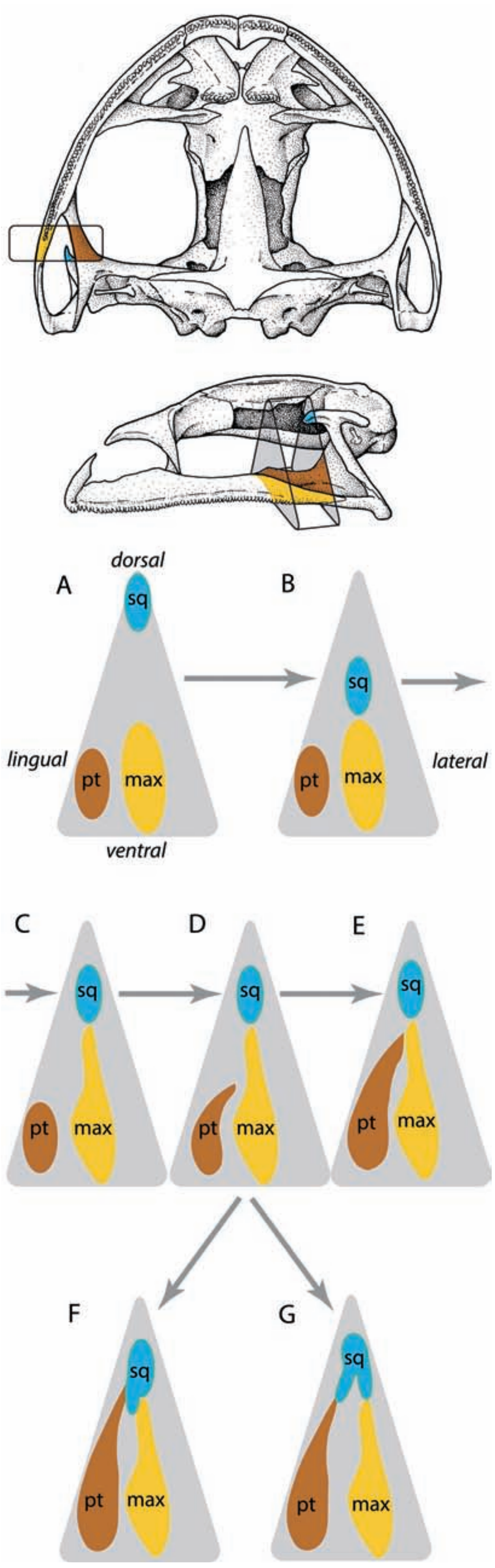

Fig. 4.8 Suspensory apparatus in *Gastrotheca*. In the ventral (*top*) and lateral (*immediately below top*) views of the skull, the plane of the schematic section through the parts of the suspensory apparatus is shown. Brown indicates the anterior ramus of the pterygoid (pt); yellow, the maxilla (max) in the postorbital region; and blue, the zygomatic ramus of the squamosal (sq). A: the common arrangement among anurans in which the pterygoid bears no dorsal flange, a postorbital process of the maxilla is missing, and the zygomatic ramus does not articulate with the maxilla. B: the zygomatic ramus is complete to the maxilla, but neither the maxilla nor the pterygoid is modified. C: with the presence of a postorbital process on the maxilla, the maxilla articulates with a shorter zygomatic ramus than in the preceding diagram. D: similar to C, except for the presence of a broad low flange on the pterygoid. E: the higher pterygoid flange articulates with the medial surface of the postorbital process of the maxilla. F: the higher pterygoid flange articulates with the medial surface of the zygomatic ramus of the squamosal. G: an unusual situation in which the zygomatic ramus of the squamosal bifurcates distally, with one branch articulating with the pterygoid and the other with the maxilla. Drawings by L. Trueb.

Gastrotheca fissipes, *fulvorufa*, *nebulanastes*) to a broadly triangular process that is moderate in height (e.g., *G. ernestoi*, *lojana*, *microdiscus*, *peruana*). Other taxa have a high dorsal process that may be uniform in width with either a blunt end (e.g., *G. nicefori* and *G. riobambae*) or an acuminate terminus (e.g., *G. angustifrons* and *G. dendronastes*). In most other *Gastrotheca* the process is high, acuminate, and recurved. The process usually articulates with the medial surface or medial branch of the zygomatic ramus of the squamosal (e.g., *G. albolineata*, *carinaceps*, *orophylax*; Fig. 4.8). In some species (e.g., *G. bufona*, *nebulanastes*, *nicefori*) the dorsal process articulates with the medial surface of the postorbital process of the maxilla, but not with the zygomatic ramus of the squamosal. In others the process articulates with both the postorbital process of the maxilla and the zygomatic ramus of the squamosal (e.g., *G. dunni*, *ernestoi*, *espeletia*, *helenae*, *piperata*, *riobambae*).

Bones of the Palate

Well-developed neopalatines underlying the plana antorbitalae are characteristic of *Gastrotheca* (Fig. 4.9). The broad neopalatine invests the ventral, as well as the anterior, margin of the planum to form a bony posterior margin to the choana. The bone articulates with the lingual face of the pars facialis of the maxilla; although the lateral edge may be extended anteriorly along the pars facialis, it is not expanded posteriorly to articulate with the end of the anterior ramus of the pterygoid. The neopalatine varies in two significant features: (1) its length, expressed as the degree of medial separation of the bones beneath the sphenethmoid, and (2) the configuration of the ventral surface of the bone beneath the planum antorbitale.

In most species of *Gastrotheca* the neopalatines terminate medially at the edge of the bony sphenethmoid; thus the termini are widely separated and lateral to the orbitonasal foramina (Fig. 4.9). The bones have a greater overlap with the sphenethmoid and a narrower separation from one another in taxa such as *G. antomia*, *ovifera*, *pacchamama*, *recava*, and a few others in which the neopalatines terminate at the level of the orbitonasal foramina. The neopalatines are narrowly separated from one another medially in *G. dendronastes*, *galeata*, *marsupiata*, *nicefori*, *psychrophila*, and *weinlandii*.

The ventral surface of the neopalatine usually bears a low rounded ridge in *Gastrotheca*. The ridge is somewhat elaborated and has an irregularly scalloped edge in some taxa (e.g., *G. excubitor*, *guentheri*, *lateonota*, *mar-*

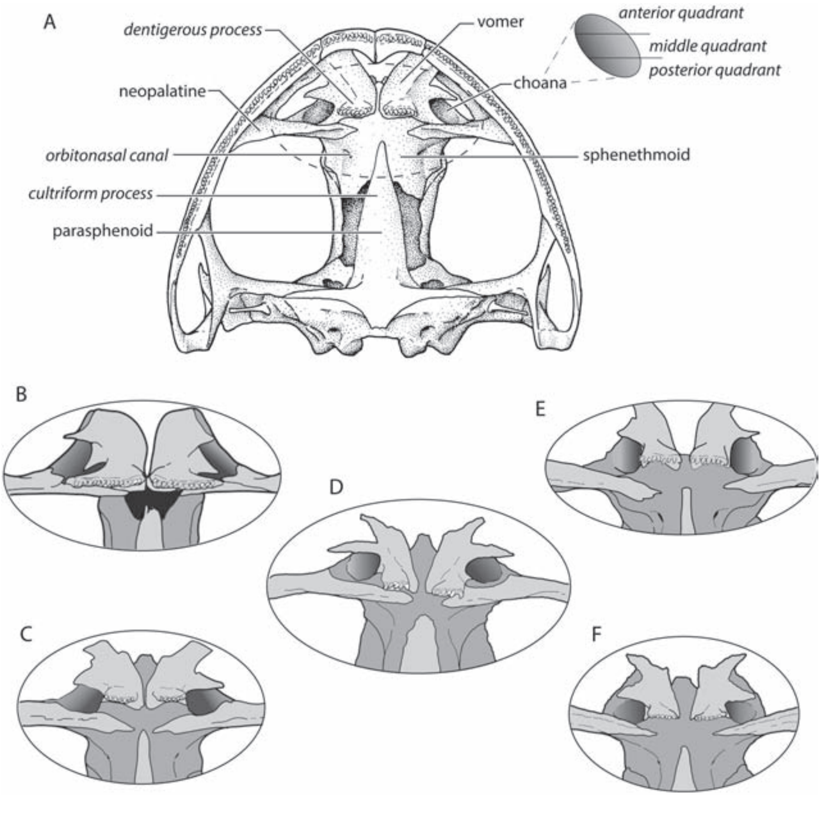

Fig. 4.9 Diversity of the anterior palate in *Gastrotheca* and its allies. Roman typeface is used to label the bones, whereas italics are used to designate a part of a bone or the skull (e.g., process, quadrant). A: *G. walkeri*, with the dashed oval indicating the area of the skull shown in B–F. A schematic of the choana (*right of the skull*) indicates the quadrants of the choana between which the dentigerous processes might lie. B: *Cryptobatrachus conditus*. C: *G. dendronastes*. D: *G. helenae*. E: *G. carinaceps*. F: *G. testudinea*. Note the spatial relationships between the vomers, the medial ends of the neopalatines, and the anterior tip of the parasphenoid. Variation is also evident in the sizes and proportions of the pre- and postchoanal processes of the vomers, and the position of the dentigerous processes relative to the choanae. Drawings by L. Trueb.

supiata, *orophylax*). In other taxa, the neopalatine bears a ventral flange, the edge of which varies from being irregularly scalloped to serrated and denticulate (e.g., *G. espeletia*, *galeata*, *lojana*, *ovifera*, *recava*).

Vomers (Fig. 4.9) are present in all *Gastrotheca* and typically are well developed and dentate; the palatal bones support the olfactory organ anterior to the sphenethmoid. The anterior plate of the vomer floors the anterolateral portion of the olfactory organ. The plate clearly extends to the maxillary arcade in most species of *Gastrotheca*, but in some species (e.g., *G. aureomaculata*, *carinaceps*, *christiani*, *helenae*, *monticola*, *plumbea*, *pseustes*) it is not clearly ossified adjacent to the upper jaw.

The pre- and postchoanal processes of the vomer support the anterior and the medial margins of the choana (Fig. 4.9). In most *Gastrotheca* the prechoanal process is long; it supports most of the anterior margin of the choana but is clearly separated from the lingual surface of the pars facialis of the maxilla. In a few species (e.g., *G. dendronastes*, *ernestoi*, *excubitor*, *galeata*, *peruana*) the prechoanal process nearly touches the lingual surface of the pars facialis. It is unclear whether the proximity of the maxilla and the vomerine process is a function of the length of the process or the configuration of the rostrum and the pars facialis of the maxilla. Rarely, the prechoanal process is short and does not support the complete anterior margin of the choana (e.g., *G. bufona*, *gracilis*, *guentheri*). The postchoanal process lies adjacent to the bony sphenethmoid along the medial margin of the choana and adjacent to the bony sphenethmoid. It is short in some species (e.g., *G. albolineata*, *chrysosticta*, *marsupiata*, *monticola*, *riobambae*) and supports only the anteromedial margin of the choana. In others (e.g., *G. ernestoi*, *lateonota*, *nicefori*, *testudinea*) it is larger, supporting more than half of the medial choanal margin. In a few taxa (e.g., *G. dunni*, *espeletia*, *lojana*, *ovifera*, *peruana*, *walkeri*) the postchoanal ramus of the vomer supports the entire medial margin of the choana.

With a few exceptions in which the dentigerous processes of the vomer are markedly small (e.g., *Gastrotheca bufona*, *espeletia*, *excubitor*, *galeata*, *piperata*, *riobambae*, *ruizi*), these processes are moderately large to large in most *Gastrotheca*. The orientation of the dentigerous processes is variable. In some taxa (e.g., *G. abdita*, *bufona*, *galeata*, *griswoldi*, *rebeccae*, *walkeri*) the medial ends of the processes clearly lie posterior to the lateral ends (i.e., \ /), whereas in a few the medial angle is obtuse (e.g., *G. andaquiensis*, *aureomaculata*, *carinaceps*, *christiani*, *ochoai*). In most taxa the dentigerous processes are transverse; rarely (e.g., *G. antomia*), the medial ends lie anterior to the lateral ends (i.e., / \).

The position of the dentigerous processes of the vomer (Fig. 4.9) varies relative to the position of the choanae. The oval choana is circumscribed by the leading edge of the neopalatine posteriorly and by the post- and prechoanal processes of the vomer medially and anteriorly, respectively. The dentigerous processes of a few *Gastrotheca* are located at a level medially adjacent to the anterior quarter of the longitudinal length of the choana (e.g., *G. cornuta*, *fissipes*, *lateonota*, *testudinea*, *walkeri*). More commonly, the processes are located at approximately the midlevel of the choana (e.g., *G. christiani*, *ernestoi*, *monticola*, *nebulanastes*, *nicefori*). In some the processes are between the posterior portions of the choanae (e.g., *G. abdita*, *excubitor*, *galeata*, *gracilis*, *monticola*, *ruizi*), and in a few taxa they are posterior to the choanae (e.g., *G. argenteovirens*, *chrysosticta*, *piperata*, *weinlandii*).

The parasphenoid is well developed in all *Gastrotheca* and frequently synostosed to the overlying prootics and exoccipitals, thereby obscuring the borders of the bone in the otic region (Fig. 4.10). There is some variation in the configuration of the cultriform process of the parasphenoid. The process always is long and usually terminates slightly posterior to the levels of the neopalatines; in a few species (e.g., *G. galeata*, *marsupiata*, *ochoai*, *ruizi*, *trachyceps*, *weinlandii*), the cultriform process terminates between the neopalatines. The process narrows in the anterior part of the orbit in all taxa. In some the sides of the process tend to be laterally concave, and the narrowing anterior to the optic fenestra is gradual. In other taxa the process narrows abruptly, anterior to the optic fenestra. The anterior terminus of the cultriform process is acuminate in most *Gastrotheca*, but in a few species (e.g., *G. bufona*, *carinaceps*, *chrysosticta*, *pseustes*, *peruana*) it is blunt.

Mandible

The lower jaw consists of the angulosplenial, which invests the ventral and lingual surfaces of Meckel's cartilage, and the dentary along the labial surface of the cartilage (Fig. 4.5). The mandibular symphysis of the jaw is composed of a pair of mentomeckelian bones that are separated by dense connective tissue. The lower jaw is quite unremarkable in all *Gastrotheca* (except *G. guentheri*), the only fossil or Recent anuran known to possess teeth on the dentary. These teeth are socketed, pedicellate, and bicuspid, as are the maxillary teeth.

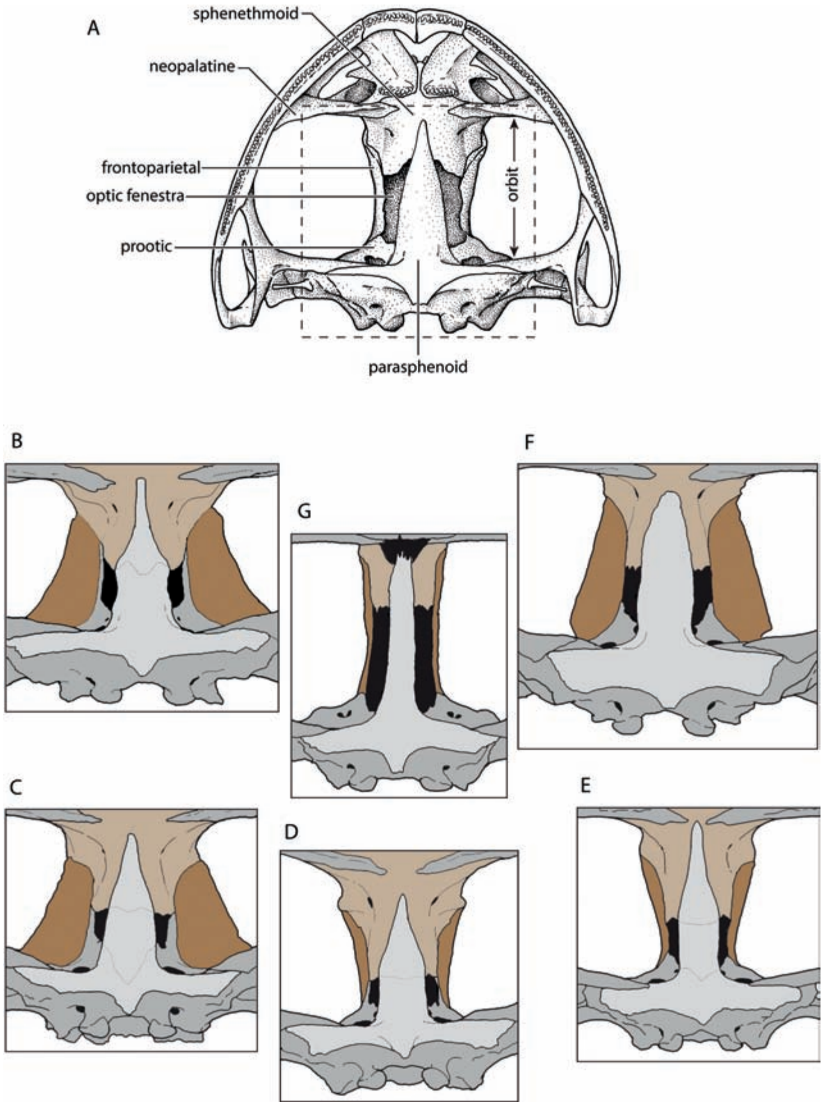

Fig. 4.10 Diversity of the braincase region in *Gastrotheca* and its allies. A: *G. walkeri*, with the dashed rectangle indicating the area of the skull shown in B–E. B: *G. carinaceps*. C: *G. testudinea*. D: *G. longipes*. E: *G. dendronastes*. F: *G. helenae*. G: *Cryptobatrachus conditus*. The varying shapes of the sphenethmoid are apparent; note the abrupt narrowing of the cultriform process anterior to the optic fenestra in B, in contrast to all others except D, in which the narrowing is semiabrupt. The degree of ossification of the bony sphenethmoid, as measured by its posterior extent, varies from the anterior part of the orbit (G, A) to the midorbit (B, F) to the posterior part of the orbit (D). Dark brown indicates the frontoparietal. In G, there is no supraorbital flange, whereas there are narrow flanges in D and E and wide flanges in B, C, and F. Drawings by L. Trueb.

Characterization of *Gastrotheca*

There is no single cranial osteological synapomorphy that unites members of this genus and distinguishes it from all other anurans. To students of anuran morphology, this should come as no surprise. Anuran morphological characters are rife with homoplasy, no doubt because once the neobatrachian ancestor achieved an overall architecture that enabled it to leap and catapult its tongue from its mouth to feed, further changes were highly constrained. This is particularly true of the postcranial skeleton of *Gastrotheca*; the differences are slight and insufficient to characterize individual species. Yet this is not the case for the cranium; males and females of each species have a unique combination of adult cranial characters that distinguish them from all other *Gastrotheca*.

Commonalities shared by most, but not all, *Gastrotheca* include the following cranial features.

1. The skin of the skull is co-ossified or firmly adherent to the bones below in all taxa, except some small frogs, such as *G. ochoai*.
2. The dorsally exposed sphenethmoid is exostosed in most species.
3. The pattern of cranial exostosis usually is uniform across the skull table.
4. The nasals usually articulate with the frontoparietals.
5. The frontoparietals have a complete medial articu-

lation with one another posterior to the sphenethmoid in nearly all taxa.
6. A supraorbital flange usually is present on the frontoparietal.
7. The presence of the preorbital process of the maxilla is obscured by an expansion of the pars facialis in most species.
8. The zygomatic ramus of the squamosal is complete to the maxilla in most taxa.
9. The medial ends of the neopalatines tend to be widely separated ventral to the sphenethmoid.
10. The anterior ramus of the pterygoid has a dorsal process that usually articulates with the medial surface of the zygomatic ramus of the pterygoid and/or the postorbital process of the maxilla.

Subgenus *Eotheca*

The basal subgenus of *Gastrotheca* (*G. fissipes*, *megacephala*, *prasina*, *recava*) from Brazil is characterized by a suite of cranial characters that distinguishes these taxa from all other subgenera. These large and extensively ossified species have the following characteristics.

1. A complete temporal arcade is formed by the expansion and articulation of the frontoparietal and the head of the squamosal over the otic capsule.
2. In lateral profile the snout is truncate, owing to the minimal (< 10°) posterior deflection of the alary processes of the premaxillae.
3. The maxilla bears a massive postorbital process that has a horizontal articulation with the zygomatic ramus of the squamosal.
4. The squamosal has a narrow otic plate overlapping the margin of the crista parotica beneath the temporal arcade.
5. The ends of the neopalatines extend medial to the level of the orbitonasal foramina beneath the sphenethmoid; thus the bones are moderately to narrowly separated from one another.
6. The dentigerous processes of the vomers are located forward, between the anterior parts of the choanae. All members of this clade have a fine pattern of exostosis, except *G. prasina*, which has a semicoarse pattern.

Subgenera *Cryptotheca* + *Amphignathodon* + *Australotheca*

These three subgenera of *Gastrotheca* are united by three features that distinguish them from all other members of the genus.

1. The carotid canal is open in all taxa except *Amphignathodon weinlandii*, in which it is partially closed.
2. The otic plate of the squamosal is well developed, in contrast to that of other subgenera; it has a moderate to broad overlap of the crista parotic of the otic capsule.
3. The frontoparietal either lacks an otic flange or has a small poorly developed flange (*G. guentheri* and *G. helenae*).

Subgenus *Cryptotheca*

Gastrotheca walkeri is probably the least-typical member of *Gastrotheca* in terms of its cranial osteology, which, in many respects, is reminiscent of the less-robust skulls of *Stefania* and markedly distinct from the heavily casqued crania of *Amphignathodon*, *Australotheca*, and *Eotheca*. The cranium is exostosed in a coarse low pattern, but the sphenethmoid is smooth and unornamented. The nasals lack a medial articulation with one another and do not articulate with the frontoparietals. The latter have an incomplete medial articulation with one another and bear only an inconspicuous supraorbital flange. There is no posterolateral elaboration of the frontoparietal in the otic region. Owing to the deflection of the alary processes of the premaxilla (31°–45°), the snout is not markedly thick and truncate. The pars facialis of the maxilla is less expanded than in most congeners of this species; thus the preorbital process in *G. walkeri* is distinct. The squamosal lacks a dorsal crest, and the zygomatic ramus does not articulate with the maxilla. The neopalatine is unornamented ventrally, and the anterior ramus of the pterygoid lacks a dorsal process.

Subgenus *Amphignathodon*

This subgenus consists of two groups: (1) the *Gastrotheca weinlandii* + *G. guentheri* + *G. antomia* clade, and (2) the [*G. cornuta* + *G. dendronastes*] clade + [*G. helenae* + *G. longipes*] clade. *G. guentheri* differs from all other living anurans in the possession of pedicellate bicuspid teeth on the dentary. *G. weinlandii* differs from other members of this group in having a partially closed carotid canal. The *G. cornuta–helenae* clades have robust vomers, with the prechoanal portion of the bone extending to the maxillary arcade. The node uniting *G. cornuta* and *G. dendronastes* is defined by the presence of a visible postorbital process on the maxilla and long spinous medial palatine processes on the premaxillae. In the *G. helenae* + *G. longipes* clade, the postorbital process of the maxilla is better developed than in its sister clade; it is high and broad and has a horizontal articulation with the zygomatic ramus of the squamosal. This clade also is distinguished by having a parasphenoid that narrows abruptly anterior to the optic fenestra, in contrast to other members of the subgenus.

Gastrotheca longipes has a less-robust skull than do its sister taxa, and it shares many features with *G. walkeri* and *Stefania*, suggesting that its skull structure is the result of several reversals that might have been manifested through arrested development. For example, there is no evidence of exostosis beyond the vermiform pattern of internal ossification of the sphenethmoid. The nasals do not articulate with one another medially and lack articulations with the frontoparietals. The latter have neither a supraorbital flange nor posterolateral development in the otic region. The footplate of the stapes is symmetrical.

Subgenus *Australotheca*

The four members of these Brazilian *Gastrotheca* have vomerine dentigerous processes that are located at the midlevel of the choanae. The *G. ernestoi* + *fulvorufa* + *microdiscus* clade is further characterized by four apomorphies. First, the quadratojugal is short. Second, the cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra. Third, the medial ends of the neopalatines are narrowly separated from one another beneath the sphenethmoid. Fourth, the postchoanal process of the vomer does not form the entire medial margin of the choana, because it is only moderately long. *Australotheca* and its more derived allies have a long articulation between the pars facialis of the maxilla and the ventrolateral margin of the vomer; in most, these bones articulate for about 75% of the length of the rostrum.

All *Australotheca* have sculptured sphenethmoids and a uniform pattern of semicoarse to coarse pit-and-ridge sculpturing across the skull table. The nasals are not synostosed with the frontoparietals. The latter bear a wide supraorbital flange, but the development of the otic flange is variable. Posterolaterally, the frontoparietal covers but is not synostosed with the anterior epiotic eminence; thus the carotid canal is open. The squamosal has a narrow dorsal crest; in most taxa, a wide otic plate invests the crista parotica. The development of the zygomatic ramus of the squamosal is variable, although the ramus is complete to the maxilla in all taxa. The neopalatines of this lineage are unornamented and smooth ventrally.

Subgenus *Edaphotheca*

This monotypic subgenus is represented by *Gastrotheca galeata*, an anuran with a highly elaborated osseous skull, characterized by a unique suite of cranial characters and bearing no obvious morphological similarities with its sister taxa. It is one of the few *Gastrotheca* with a heterogeneous pattern of fine pit-and-ridge dermal sculpturing across the skull table, which is heavily synostosed (i.e., the nasals, the sphenethmoid, and the frontoparietals). The otic flange is complete to the broad head of the squamosal, forming a complete temporal arcade, and the carotid canal is partially closed. The alary processes of the premaxillae are deflected posteriorly at an angle between 31° and 45°, producing a slender tapered snout in lateral profile. The pars facialis of the maxilla extends forward around the premaxillae to come in contact with the alary process of that bone. Despite the hyperossification of this species, the maxilla lacks a postorbital process and possesses a short articulation with the quadratojugal; the sphenethmoid is short, terminating anterior to the midpoint of the orbit. The stapedial footplate is asymmetrical, with the dorsal part being about three times larger than the ventral portion. The cultriform process of the parasphenoid is long, terminating anterior to the level of the neopalatines, which are narrowly separated from one another ventral to the sphenethmoid. The prechoanal process of the vomer extends laterally to contact the inner surface of the maxilla; the dentigerous processes of the vomer are minute and located between the posterior parts of the choanae. The anterior pterygoid ramus lacks a dorsal process and, hence, an articulation with the squamosal.

Subgenera *Duellmania* and *Gastrotheca*

The two most phylogenetically advanced subgenera of *Gastrotheca*—*Duellmania* and *Gastrotheca*—are exceedingly complex morphologically and challenging to characterize. Moreover, a comparison of the trees resulting from an analysis of molecular data and combined morphological and molecular data (Fig. 4.11) reveals somewhat different arrangements within each subgenus, although the membership of each remains much the same. When inspecting these trees, it is important to note that the sampling differs. Thus molecular data were available for some taxa not represented by skeletal material, and some skeletal material, in turn, was available for taxa for which there were no molecular data.

Subgenus *Duellmania*

This morphologically diverse subgenus of *Gastrotheca* is difficult to define osteologically; two weak characters unite all but two taxa. First, members of this subgenus

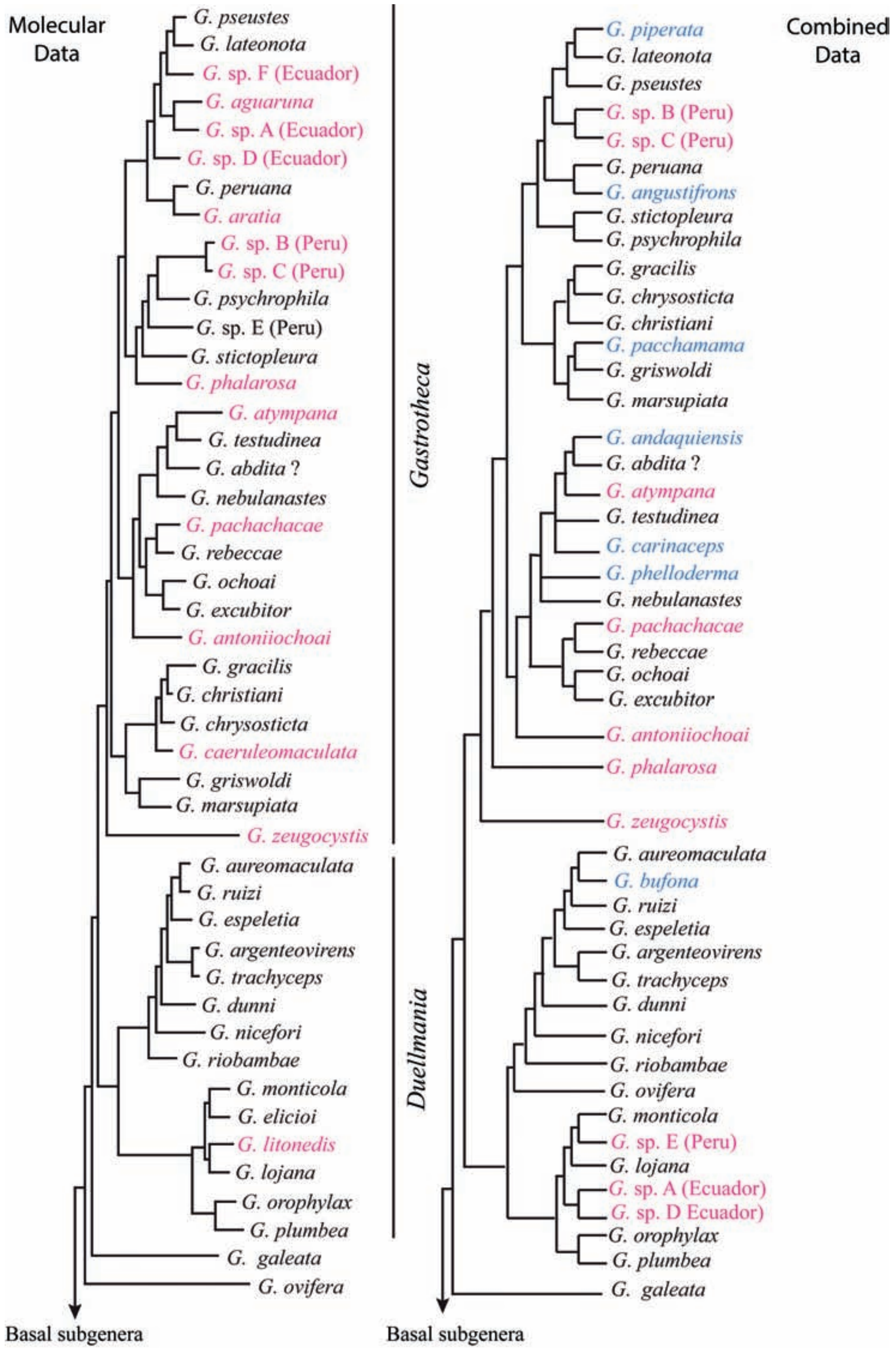
Molecular Data
Combined Data
Gastrotheca
Duellmania
G. pseustes
G. lateonota
G. sp. F (Ecuador)
G. aguaruna
G. sp. A (Ecuador)
G. sp. D (Ecuador)
G. peruana
G. aratia
G. sp. B (Peru)
G. sp. C (Peru)
G. psychrophila
G. sp. E (Peru)
G. stictopleura
G. phalarosa
G. atympana
G. testudinea
G. abdita ?
G. nebulanastes
G. pachachacae
G. rebeccae
G. ochoai
G. excubitor
G. antoniiochoai
G. gracilis
G. christiani
G. chrysosticta
G. caeruleomaculata
G. griswoldi
G. marsupiata
G. zeugocystis
G. aureomaculata
G. ruizi
G. espeletia
G. argenteovirens
G. trachyceps
G. dunni
G. nicefori
G. riobambae
G. monticola
G. elicioi
G. litonedis
G. lojana
G. orophylax
G. plumbea
G. galeata
G. ovifera
Basal subgenera
G. piperata
G. lateonota
G. pseustes
G. sp. B (Peru)
G. sp. C (Peru)
G. peruana
G. angustifrons
G. stictopleura
G. psychrophila
G. gracilis
G. chrysosticta
G. christiani
G. pacchamama
G. griswoldi
G. marsupiata
G. andaquiensis
G. abdita ?
G. atympana
G. testudinea
G. carinaceps
G. phelloderma
G. nebulanastes
G. pachachacae
G. rebeccae
G. ochoai
G. excubitor
G. antoniiochoai
G. phalarosa
G. zeugocystis
G. aureomaculata
G. bufona
G. ruizi
G. espeletia
G. argenteovirens
G. trachyceps
G. dunni
G. nicefori
G. riobambae
G. ovifera
G. monticola
G. sp. E (Peru)
G. lojana
G. sp. A (Ecuador)
G. sp. D Ecuador)
G. orophylax
G. plumbea
G. galeata
Basal subgenera

Fig. 4.11 Hypothesized phylogenies of the subgenera *Duellmania* and *Gastrotheca*. *Left*: molecular phylogeny. *Right*: tree based on combined molecular and osteological data. Taxa in red are ones for which there are no osteological data; those in blue on the combined data tree are ones for which there are no molecular data.

possess moderately deflected alary processes on the premaxillae, which produces a thick but not truncate snout; the deflection is much greater and the profile of the snout thinner in *G. ruizi* than in either any other member of the subgenus or *Gastrotheca* as a whole. Second, all taxa have a narrow otic plate, except *G. bufona*, a taxon not included in the molecular analysis.

All members of the *Gastrotheca monticola* clade (*G. monticola* sp. B, *lojana*, *orophylax*, and *plumbea*; Fig. 4.11) have neopalatines that are widely separated below the sphenethmoid. Likewise, they have parasphenoids with cultriform processes that narrow abruptly anterior to the optic fenestra; they share this trait with both *Edaphotheca* and most *Gastrotheca*. The clade (except *G. lojana*) has neopalatines with a low irregular ventral ridge. The group composed of *G. monticola* sp. A, sp. B, and *lojana* has a squamosal with a wide dorsal head, but the zygomatic ramus is narrow in its lateral aspect. Within this lineage, the postorbital process of the maxilla of *G. orophylax* and *G. plumbea* is high and broad in its lateral aspect and has a horizontal articulation with the zygomatic ramus of the squamosal; in addition, the articulation of the pars facialis of the maxilla and the ventrolateral edge of the nasal is only about 50% complete.

Although *Gastrotheca ovifera* is basal to the subgenera *Edaphotheca*, *Duellmania*, and *Gastrotheca* in the molecular tree (Fig. 4.11), in the combined analysis of morphological and molecular data, *G. ovifera* is resolved as the sister taxon to a clade composed of *G. argenteovirens*, *aureomaculata*, *bufona*, *dunni*, *espeletia*, *nicefori*, *riobambae*, *ruizi*, and *trachyceps*. All members of this group (except *G. nicefori*) have parasphenoids with cultriform processes that narrow gradually anterior to the optic fenestra, and all (except *G. espeletia*) have a partially closed carotid canal; it is open in *G. espeletia*. The group comprising *G. argenteovirens*, *aureomaculata*, *bufona*, *espeletia*, *ruizi*, and *trachyceps* lacks an evident postorbital process on the maxilla, and all of these taxa (except *G. trachyceps*) have a long spinous medial palatine process on the premaxilla. *G. argenteovirens*, *dunni*, *espeletia*, and *trachyceps* have a prominent postorbital process on the maxilla that has a broad horizontal articulation with the zygomatic ramus of the squamosal. *G. dunni*, *espeletia*, and *trachyceps* have a neopalatine with a low irregular ridge ventrally, whereas in *G. aureomaculata*, *bufona*, *espeletia*, and *ruizi*, the neopalatine bears a distinct ventral flange. In *G. argenteovirens*, *espeletia*, and *trachyceps*, the nasals are synostosed with the sphenethmoid, whereas in *G. aureomaculata* and *G. bufona*, the anterior terminus of the cultriform process of the parasphenoid is acuminate, rather than blunt, and the pattern of dermal sculpturing is heterogeneous across the skull table. The frontoparietals of both taxa extend over the anterior epiotic eminence and part of the posterior eminence. Both have a pattern of vermiform ossification in the sphenethmoid; the skull table of *G. bufona* is smooth, whereas that of *G. aureomaculata* has a semicoarse pattern of shallow pits and low rounded ridges.

Subgenus *Gastrotheca*

Based on analyses of combined osteological and molecular data, this subgenus is represented by three major clades: (1) *Gastrotheca zeugocystis*, (2) *G. phalarosa*, and (3) the more advanced allies of the former taxa. Unfortunately, osteological specimens of *G. zeugocystis* and *G. phalarosa* were unavailable; thus osteological characterization of these taxa and their ancestral nodes is not possible. The placement of *G. zeugocystis* is the same in both the combined and molecular trees (Fig. 4.11). *G. phalarosa* is basal to all remaining taxa in the subgenus (except *G. zeugocystis*) in the combined tree, whereas it is nested amid more advanced taxa in the molecular tree. The remaining species of *Gastrotheca*, all of which have a semicoarse pit-and-ridge pattern of dermal sculpturing on the skull table and a tendency toward reduced ossification of the skull, are represented by two major lineages, as opposed to four in the molecular results. One is composed of *G. antoniiochoai* and its sister-group, herein termed the *G. excubitor* clade, and the other, the *G. marsupiata* clade.

Osteologically, the *Gastrotheca excubitor* clade (exclusive of *G. antoniiochoai*, for which, in this discussion, a skeleton was unavailable) represents a montage of plesiomorphic characters. The *G. excubitor* group—[*G. excubitor* + *G. ochoai*] and [*G. pachachacae* + *G. rebeccae*]—has neopalatines that have a moderate medial separation ventral to the sphenethmoid and bear a low irregular ventral ridge. The dentigerous processes of the vomers are located at the posterior level of the choanae. The sister taxa *G. excubitor* and *G. ochoai* lack a supraorbital flange on the frontoparietal. Three distantly related species in this lineage exhibit multiple signs of independent reversals to a less osseous and robust skull: *G. andaquiensis*, *nebulanastes*, and *ochoai*. In all three, the pars facialis of the maxilla has a short articulation with the nasal. *G. nebulanastes* and *G. ochoai* have small nasals that do not articulate medially; likewise, the nasals do not articulate with the frontoparietals, and the frontoparietals have an incomplete medial articulation. The zygomatic ramus of the squamosal is slender in *G. andaquiensis* and *G. nebulanastes*, and the ramus is incomplete in *G. ochoai*. Both *G. andaquiensis* and *G. ochoai* lack an otic flange on the frontoparietal. The sister species *G. abdita* and *G. andaquiensis* have an evident postorbital process on the maxilla.

The *Gastrotheca marsupiata* clade is somewhat more tractable than its sister-group in terms of its osteological features. It is characterized by lack of supraorbital and otic flanges on the frontoparietal and an open carotid canal, all of which represent diminished ossification of the cranium. Two sister-groups compose this clade in the combined tree (Fig. 4.11). The more narrowly defined *G. marsupiata–G. gracilis* lineage is less well ossified than its sister clade, the *G. psychrophila–G. piperata* lineage. The *G. marsupiata–G. gracilis* clade has a high truncate snout in lateral profile, owing to the minimal posterior deflection of the alary processes of the premaxillae, and the postorbital process on the maxilla is either absent or scarcely evident. Additionally, these frogs lack a supraorbital flange on the frontoparietal; the carotid canal is open and, in most of them, the frontoparietal does not cover the epiotic eminences. In contrast, members of the *G. psychrophila–G. piperata* clade have a conspicuous supraorbital flange, and most have a partially closed carotid canal and a frontoparietal that covers the anterior epiotic eminence. In addition, the alary processes of the premaxillae are deflected posteriorly, such that the snout is not markedly truncate in lateral profile.

One species-pair defined by osteological features is evident in the *Gastrotheca marsupiata* clade: *G. griswoldi* and *G. pacchamama* share several features associated with reduction of the osseous cranium. The skulls are smooth, not exostosed. The nasals do not articulate with the frontoparietals, and the latter lack a complete medial articulation. The head of the squamosal lacks a dorsal crest, and the anterior ramus of the pterygoid lacks a dorsal process.

Within the *Gastrotheca psychrophila–G. piperata* clade, both *G. angustifrons* and *G. peruana* possess a heterogeneous pattern of dermal sculpturing and a smooth non-exotosed sphenethmoid. The nasals do not articulate with the frontoparietals, and the latter lack a complete medial articulation. The quadratojugal is short. *G. lateonota* and *G. piperata* are alike in having hyperossified nasals; the bones are fused to one another medially, and the sphenethmoid posteriorly.

This analysis of evolutionary trends in cranial osteology in *Gastrotheca* has, on the one hand, been a journey of frustration, and, on the other, a promising exercise in the informative power of combined data on our understanding of a particular group of anurans. The frustration emanates from the many taxa for which little or no morphological information is available, from our meager knowledge of variation between sexes and within and between populations, and from our exceedingly limited knowledge of ontogenetic development of the skeleton among members of *Gastrotheca*. Further, we have no idea of the functional significance of the characters and character complexes that have been described here and elsewhere. All of these factors speak to the need for, and satisfaction of, producing morphological studies to complement and provide evolutionary meaning to the relationships revealed by molecular analyses.

Yet the relative ease with which genomic data can be retrieved and analyzed to produce trees provides unparalleled opportunities for morphologists to ply their trade. This has been one of the most rewarding aspects of the *Gastrotheca* project. The concordance of the molecular and osteological data in the deep phylogeny of the marsupial frogs is both informative and significant. Cranial characters can be used to unite taxa. Among the more advanced taxa, the amount of homoplasy thwarts characterization, but it also documents the enormous evolutionary plasticity of cranial development in anurans.

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5

External Morphological Features

Throughout the accounts of the genera and species, many morphological characters are used to distinguish and describe the taxa. Herein I present definitions and illustrations (where appropriate) of these morphological features.

Adult Frogs

Size and Proportions

Frogs of the genus *Gastrotheca* exhibit great differences in their sizes and proportions. Several large species attain maximum snout–vent lengths of more than 75 mm, and females of one species attain a maximum known snout–vent length of 110 mm. In contrast, adult males of some small species have snout–vent lengths of less than 30 mm.

In the accounts of the species, I have used general terms to describe size. These arbitrary terms are defined here. The designation large is applied to frogs in which the snout–vent length is greater than 70 mm in males and/or greater than 75 mm in females, whereas moderately large is applied to species in which the snout–vent length is 60 mm in males and/or greater than 65 mm in females. In medium-sized species, the snout–vent length is greater than 45 mm in males and/or greater than 50 mm in females. Those species in which males have snout–vent lengths of less than 45 mm and/or females less than 50 mm are termed moderately small, whereas the term small is applied to those species in which the snout–vent length of males is less than 30 mm and less than 40 mm in females.

One of the most striking differences in proportions is the length of the hind limb. In the arboreal species of the subgenus *Amphignathodon*, the length of the tibia is more than 60% of the snout–vent length; these species also have long feet, but the foot length is noticeably less than the tibia length (Table 5.1). In contrast, terrestrial species have proportionately shorter limbs. The tibia length ranges from 40.3% to 48.7% in 15 terrestrial species; in nearly all of these species the foot is longer than the tibia. At least some of these species are walkers or move by short hops, in contrast to the leaping abilities of the arboreal

Table 5.1 Selected proportions of measurements of species of *Gastrotheca*. Abbreviations: HL = head length; HW = head width; IOD = interorbital distance; SSD = sexual size dimorphism (female SVL divided by male SVL); SVL = snout–vent length. Numbers are means, with the sexes combined, except for maximum SVLs.

	Maximum SVL								
Species	Males	Females	SSD	Tibia/SVL	Tibia/foot	Eyelid/IOD	HW/SVL	HL/SVL	HW/HL
G. abdita	36.0	46.2	1.28	47.2	1.00	0.57	37.6	33.7	1.12
G. aguaruna	46.8	50.8	1.09	48.3	0.99	0.98	38.5	36.6	1.05
G. albolineata	59.3	59.9	1.30	50.0	1.12	0.48	39.8	37.0	1.08
G. andaquiensis	62.0	76.8	1.22	62.6	1.17	0.73	36.4	33.1	1.10
G. angustifrons	73.2	91.8	1.15	65.4	1.26	0.87	36.9	34.7	1.06
G. antomia	54.5	58.7	1.08	60.4	1.19	0.69	40.7	32.5	1.24
G. antoniiochoai	27.0	32.5	1.21	50.6	1.07	0.74	34.3	31.6	1.04
G. aratia	48.1	56.8	1.23	46.6	1.00	0.87	34.9	33.9	1.03
G. argenteovirens	53.4	58.3	1.09	47.6	1.02	0.65	36.9	32.7	1.13
G. atympana	46.7	—	—	51.8	1.27	0.42	36.8	32.3	1.14
G. aureomaculata	71.6	72.6	1.01	50.7	1.03	0.64	37.3	33.6	1.11
G. bufona	66.8	—	—	58.7	1.21	0.72	42.2	34.1	1.24
G. caeruleomaculata	33.7	41.6	1.23	47.6	1.02	0.82	34.9	32.1	1.05
G. carinaceps	—	79.7	—	54.8	1.11	0.52	36.6	33.2	1.12
G. christiani	38.8	39.1	1.01	49.7	1.02	0.85	34.5	31.3	1.10
G. chrysosticta	36.1	36.2	1.00	47.2	1.06	0.86	34.2	30.9	1.11
G. cornuta	88.1	77.4	1.06	63.1	1.31	0.77	38.3	34.3	1.11
G. dendronastes	74.4	73.5	1.03	64.8	1.22	0.89	39.0	35.5	1.10
G. dunni	43.1	54.7	1.27	45.7	0.98	0.64	36.7	33.9	1.08
G. ernestoi	68.0	69.6	1.04	49.5	1.10	0.61	37.1	35.4	1.08
G. espeletia	52.6	51.9	0.99	38.2	0.87	0.89	36.7	33.1	1.11
G. excubitor	42.5	42.0	1.07	48.7	1.05	0.66	37.5	33.5	1.12
G. fissipes	69.7	82.0	1.25	45.8	1.19	0.47	38.3	34.6	1.13
G. flamma	—	55.3	—	48.5	1.27	0.67	36.7	36.2	1.06
G. fulvorufa	68.8	76.5	1.08	54.6	1.19	0.54	36.2	34.6	1.03
G. galeata	46.0	54.8	1.17	42.3	0.99	0.50	33.8	33.0	1.04
G. gracilis	41.6	44.9	1.13	49.3	1.08	0.78	35.7	33.6	1.11
G. griswoldi	40.0	43.5	1.03	43.3	0.95	0.84	35.9	31.8	1.13
G. guentheri	70.0	82.0	1.02	62.4	1.28	0.62	41.0	35.5	1.15
G. helenae	65.8	65.0	1.05	50.5	1.04	0.52	38.8	33.9	1.15
G. lateonota	61.4	63.7	1.04	46.6	1.12	69.3	35.1	31.2	1.13
G. litonedis	52.5	62.4	1.19	44.1	0.97	78.1	35.0	32.1	1.09
G. lojana	61.0	76.1	1.25	51.0	1.14	0.64	37.9	34.0	1.11
G. longipes	70.8	88.3	1.21	61.3	1.28	0.72	35.7	33.3	1.11

continued

Table 5.1 continued

	Maximum SVL								
Species	Males	Females	SSD	Tibia/SVL	Tibia/foot	Eyelid/IOD	HW/SVL	HL/SVL	HW/HL
G. marsupiata	41.6	49.6	1.08	45.8	1.02	0.89	34.6	31.5	1.11
G. megacephala	77.8	110.0	1.33	46.4	1.13	0.47	40.9	36.2	1.13
G. microdiscus	66.9	58.3	1.02	53.2	1.12	0.59	37.9	36.9	1.04
G. monticola	58.6	73.0	1.25	51.5	1.14	0.59	37.3	32.7	1.14
G. nebulanastes	38.3	40.7	1.06	52.8	1.11	0.67	36.7	34.8	1.05
G. nicefori	74.4	81.2	1.09	51.4	1.12	0.49	39.5	34.1	1.16
G. ochoai	30.4	37.5	1.23	51.3	1.13	0.70	33.8	31.5	1.07
G. orophylax	59.1	74.0	1.25	49.6	1.04	0.50	38.5	33.7	1.14
G. ossilaginis	38.5	53.3	1.38	50.6	1.04	0.44	36.8	35.0	1.05
G. ovifera	57.8	83.0	1.43	52.5	1.15	0.44	40.6	35.1	1.16
G. pacchamama	37.0	38.0	1.02	45.2	1.12	0.78	36.2	37.3	0.97
G. pachachacae	29.2	35.3	1.21	49.9	1.02	0.85	35.8	34.1	1.05
G. peruana	52.6	56.5	1.07	42.7	1.01	0.97	35.8	32.3	1.11
G. phalarosa	45.2	—	—	42.9	1.05	0.90	37.8	33.9	1.05
G. phelloderma	43.8	57.7	1.28	45.4	0.98	0.95	41.8	39.9	1.05
G. piperata	36.3	46.8	1.29	47.7	0.99	0.84	34.4	32.9	1.05
G. plumbea	61.0	73.0	1.20	50.2	1.03	0.54	36.7	33.4	1.10
G. prasina	89.5	97.2	1.16	45.6	0.72	0.47	38.7	35.2	1.18
G. pseustes	54.4	62.4	1.15	44.5	0.96	0.85	35.1	31.5	1.11
G. psychrophila	49.9	63.5	1.27	50.1	1.03	0.58	38.2	34.1	1.12
G. pulchra	29.0	34.2	1.18	57.5	1.32	0.92	38.6	34.5	1.12
G. rebeccae	44.7	45.7	1.02	51.1	1.10	0.64	38.1	34.6	1.10
G. recava	75.4	84.9	1.13	52.4	0.76	0.95	39.9	35.4	1.13
G. riobambae	50.4	65.0	1.29	40.9	0.93	0.84	36.4	32.9	1.11
G. ruizi	67.4	78.0	1.15	44.5	0.96	0.79	33.5	31.8	1.05
G. splendens	51.3	44.7	0.87	46.3	1.12	0.60	34.8	32.0	1.09
G. stictopleura	—	68.3	—	49.8	1.12	0.63	33.8	29.7	1.14
G. testudinea	61.1	82.6	1.35	54.3	1.15	0.51	39.5	33.7	1.17
G. trachyceps	50	67.9	1.35	49.6	1.07	0.59	35.9	32.7	1.10
G. walkeri	47.3	70.0	1.48	57.9	1.29	0.79	37.4	34.8	1.07
G. weinlandii	74.2	77.9	1.05	62.0	1.22	0.63	41.7	35.4	1.18
G. williamsoni	—	53.8	—	50.6	1.29	0.63	36.1	33.5	1.08
G. zeugocystis	28.2	37.5	1.33	46.9	1.02	0.60	31.5	31.0	1.01

species. In the diagnoses in the species accounts, a distinction is made between those species having a tibia / snout–vent length ratio of more than or less than 55%. The head is wider than long in all species, but the mean head width / head length ratio is only 0.97 on *Gastrotheca pacchamama*. Another expression of head width is the ratio of the interorbital distance to the width of the eyelid. The narrowest interorbital distances are in three Andean species—*G. peruana*, *phalarosa*, and *phelloderma*—whereas the widest interorbital distances are characteristic of casque-headed species, such as *G. fissipes*, *megacephala*, and *ovifera*.

Measurements

Sixteen measurements were taken on more than 1700 adult frogs (Fig. 5.1). Poorly preserved specimens and subadults usually were not measured, so their measurements are not included in the tables in which means, ranges, and standard deviations are given for each sex. Significant differences between the sexes, resulting from analyses of variance, are noted. Ratios were determined for tibia length and foot length to snout–vent length; the proportion of eyelid width to interorbital distance was also determined. The measurements and the manner of taking them are listed in the order in which they appear in the tables.

Snout–vent length. The straight-line distance from the tip of the snout to the posterior margin of the vent.

Tibia length. The straight length of the tibia.

Foot length. The distance from the proximal edge of the inner metatarsal tubercle to the tip of the fourth (longest) toe.

Head length. The straight-line distance from the posterior edge of the jaw articulation to the tip of the snout.

Head width. The greatest width of the head.

Interorbital distance. The straight-line distance between the inner edges of the upper eyelid, usually measured as the width of the frontoparietal bones of the skull.

Eyelid width. The greatest width of the upper eyelid, measured from its medial-most edge to its outer margin.

Internarial distance. The distance between the openings of the nostrils.

Eye diameter. The greatest length of the orbit.

Eye–nostril distance. The straight-line distance from the posterior edge of the opening of the nostril to the anterior corner of the orbit.

Orbit–jaw distance. The distance from the lowermost border of the orbit to the margin of the upper lip.

Nostril–jaw distance. The distance from the lowermost border of the nostril to the margin of the upper lip.

Tympanum diameter. The greatest horizontal distance between the outer edges of the tympanic annulus.

Thumb length. The straight-line distance between the proximal edge of the prepollical tubercle and the end of Finger I.

Third finger length. The straight-line distance between the proximal edge of the palmar tubercle and the end of Finger III.

Disc width. The width of the terminal disc on Finger III.

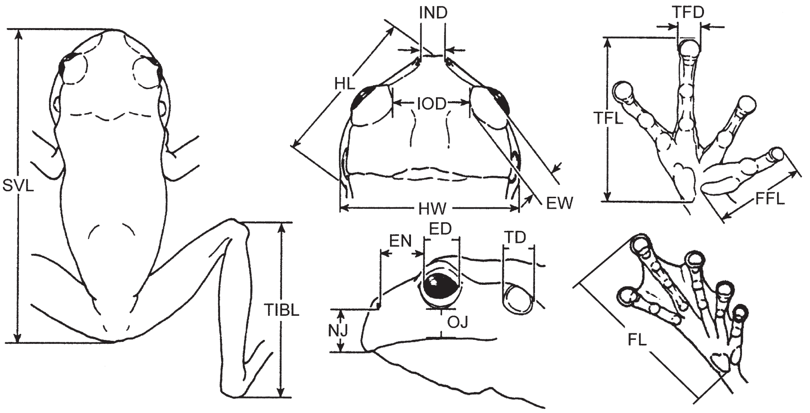

Fig. 5.1 Measurements of adult frogs. Abbreviations: ED = eye diameter, EN = eye–nostril distance, EW = eyelid width, FFL = first finger length, FL = foot length, HL = head length, HW = head width, IND = internarial distance, IOD = interorbital distance, NJ nostril–jaw distance, OJ = orbit–jaw distance, SVL = snout–vent length, TD = tympanum diameter, TFD = width of disc on third finger, TFL= third finger length, TIBL = tibia length.

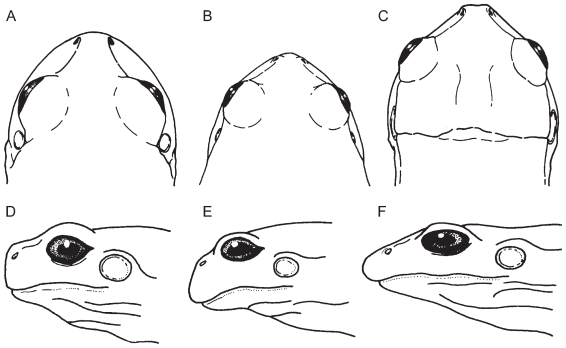

Fig. 5.2 Views of snouts. A–C: Dorsal views. A: rounded snout, *Gastrotheca gracilis* (KU 160335). B: acutely rounded snout, *G. plumbea* (KU 132421). C: truncate snout, *G. megacephala* (KU 193297). D–E: Lateral (profile) views. D: truncate snout, *G. argenteovirens* (KU 181180). E: snout inclined anteroventrally, *G. riobambae* (KU 179720). F: snout elongate, rounded, and protruding, *G. ruizi* (KU 200004).

Snout Shape

The shape of the snout is highly variable in both dorsal (top of body) and lateral (profile) views in *Gastrotheca* (Fig. 5.2). In most species the snout is rounded in dorsal view; the extremes are either bluntly rounded (e.g., *G. argenteovirens* and *G. orophylax*) or acutely rounded (e.g., *G. espeletia* and *G. marsupiata*). In three species (*G. atympana*, *flamma*, and *ossilaginis*) the snout is transversely truncate in dorsal view. The opposite outline of the extremes in dorsal view is acuminate, which is the condition in only three species (*G. ochoai*, *ruizi*, and *zeugocystis*). In lateral view, the snout most commonly is either rounded or rounded above and inclined anteroventrally to the lip. In several species, (e.g., *G. bufona*, *fissipes*, *megacephala*, *orophylax*) the snout is truncate in profile. Only in *G. ruizi* is the snout inclined and acuminate. The snout protrudes for varying distances beyond the anterior margin of the lower jaw; this is assayed by noting the position of the nostrils with respect to the anterior margin of the lower jaw.

Canthus Rostralis

The ridge between the orbit and the nostrils is straight or slightly curved, depending on the shapes of the underlying nasal bones. In cross-section, the canthus is rounded in most species, but it is angular in several species (e.g., *Gastrotheca cornuta*, *longipes*, *testudinea*) and, in some others (e.g., *G. bufona*, *flamma*, *guentheri*), it is a distinctly elevated angular ridge. The loreal region below the canthus rostralis varies from shallowly concave to nearly flat before reaching the rounded lips, which are slightly (e.g., *G. nicefori*) or distinctly (e.g., *G. galeata*) flared laterally.

Interorbital Distance

This measurement explains, in part, the width of the head and is expressed in relation to the width of the upper eyelid. In most species the interorbital distance is about 1.5–2 times the width of the eyelid, but it is about equal to the width of the upper eyelid in a few species (e.g., *Gastrotheca antoniiochoai*, *espeletia*, *gracilis*, *pulchra*). The interorbital distance is at least twice the width of the eyelid in several other species (e.g., *G. atympana*, *ernestoi*, *galeata*, *megacephala*).

Tympanum

A tympanum is absent in *Gastrotheca atympana* but is evident, with a distinct tympanic annulus, in all other hemiphractid frogs (Fig. 5.3). In most species of *Gastrotheca*, the tympanum is round, but in many species (e.g., *G. cornuta*, *guentheri*, *lateonota*, *longipes*) it is vertically ovoid. The tympanic annulus is smooth in a majority of species, but in several it is granular (e.g., *G. andaquiensis*, *flamma*, *peruana*). There is no correlation between the shape of the tympanum and the texture of the tympanic annulus.

Ulnar Tubercles

Most species lack a row of tubercles on the ventrolateral edge of the forearm. In a few species (e.g., *Gastrotheca antomia*, *helenae*, *walkeri*) the tubercles are prominent and conical, whereas in some others (*G. fissipes*, *flamma*, *guentheri*, and *trachyceps*) the subconical tubercles are less evident. In still other species having ulnar tubercles, the tubercles are small and low; there may be as few as two tubercles (*G. christiani*) to as many four (*G. longipes*).

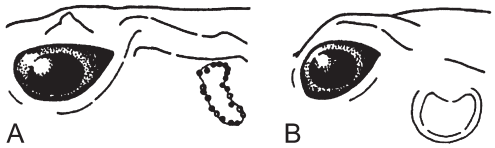

Fig. 5.3 Orbital and tympanic regions. A: vertically ovoid tympanum with granular tympanic annulus, *Gastrotheca weinlandii* (KU 154104). B: rounded tympanum with smooth tympanic annulus, *G. riobambae* (KU 179720).

Numbering of Fingers and Toes

Individual fingers and toes are identified by roman numerals. Thus the median (preaxial) finger or toe is referred to as Finger I and Toe I, respectively (Fig. 5.4). The description of the external features of the hand follows the standard practice of the median (preaxial) digit (thumb) being designated Finger I. Alberch and Gale (1985) and Fabrezi and Alberch (1996) showed that the first (preaxial) digit is lost during development, so the first digit (thumb) of anurans actually is Digit II. This arrangement is becoming standard in osteological studies. Consequently, in a description of the external features, the digits on the hand are referred to as Fingers I, II, III, and IV; the same digits in the osteological description are designated Digits II, III, IV, and V.

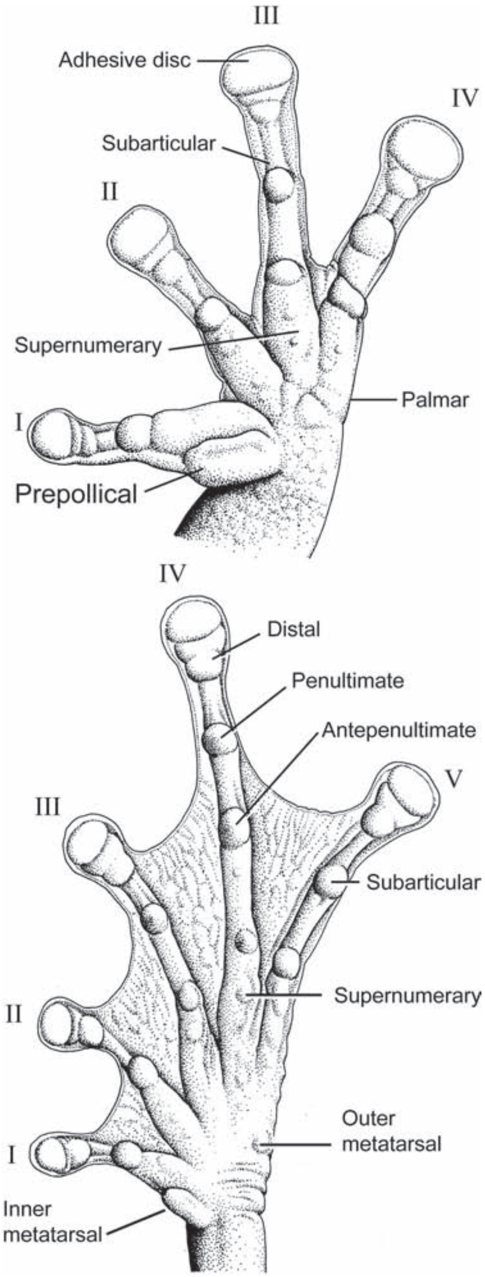
III
Adhesive disc
IV
Subarticular
II
Supernumerary
Palmar
I
Prepollical
IV
Distal
Penultimate
Antepenultimate
V
III
Subarticular
Supernumerary
II
Outer metatarsal
I
Inner metatarsal

Fig. 5.4 Palmar view of hand (*top*) and plantar view of foot (*bottom*), showing the numbering of the digits and the names of the tubercles.

Lengths of Fingers

In all hemiphractid frogs, Finger III is the longest and Finger IV is the next to longest. A considerable amount of variation exists in the comparative lengths of Fingers I and II. The relative lengths of these digits is determined by adpressing the fingers (Fig. 5.5).

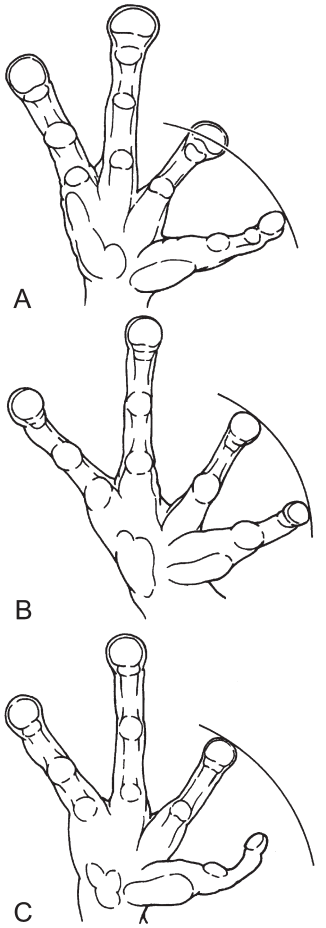

Fig. 5.5 Hands, showing the comparative lengths of Fingers I and II. A: Finger I longer than Finger II. B: Fingers I and II equal in length. C: Finger I shorter than Finger II.

Digital Discs

The round (or nearly so) terminal discs on Fingers II–IV are variable in size. In general the discs are largest in the large arboreal species and smallest in the small terrestrial species. The breadth of the disc on Finger II was measured and compared with the diameter (length) of the tympanum, and it was visually compared with the width of the penultimate segment of Finger III. The disc is barely wider than the digit in many terrestrial species (e.g., *Gastrotheca espeletia*, *phelloderma*, *riobambae*), whereas it is much wider than the digit in most arboreal species (e.g., *G. albolineata*, *fissipes*, *testudinea*). The discs on the toes are equal in size or slightly smaller than those on the fingers. The digital discs have an adhesive pad on their ventral surface; this pad is delimited by a circumferential groove.

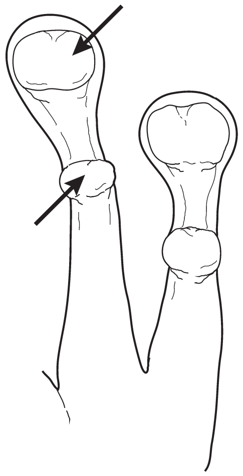

Fig. 5.6 Ventral view of two fingers of *Cryptobatrachus conditus*, showing the adhesive discs (arrows) on the terminal pad and penultimate subarticular tubercle.

Tubercles on the Hand

Usually there are two large tubercles on the palmar surface of the hand (Fig. 5.4). The outermost palmar tubercle usually is slightly elevated and commonly is bifid (e.g., *Gastrotheca andaquiensis*, *cornuta*, *orophylax*), but it is trifid in a few species (e.g., *G. bufona*, *christiani*, *pacchamama*), round in some others (e.g., *G. albolineata*, *fulvorufa*, *longipes*), cordiform in *G. antomia*, large and subconical in *G. guentheri*, and elongate in *G. galeata*. In several species (e.g., *G. argenteovirens*, *ovifera*, *weinlandii*) the palmar tubercle is low and diffuse; the tubercle is absent in *G. phalarosa* and *G. zeugocystis*. The innermost tubercle on the palm is the prepollical tubercle, which extends from the median base of the hand to the base of the first digit (thumb). The tubercle is elliptical or ovoid in shape, and it is usually slightly elevated. Some variation is notable: narrowly elliptical in *G. albolineata*, broadly ovoid in *G. trachyceps*, and massive in *G. zeugocystis*.

The tubercles under the joints in the finger are the subarticular tubercles, which are round basally and variable in size. In overall shape they are round in most species, subconical in some (e.g., *Gastrotheca espeletia*, *fissipes*, *riobambae*), conical in *G. phelloderma*, and flat in *G. aureomaculata*. In a few species (e.g., *G. abdita* and *G. helenae*) the distal subarticular tubercle is bifid. The distal subarticular tubercles on Fingers III and IV in *Cryptobatrachus* have distinct adhesive pads and circumferential grooves like those on the terminal digital discs (Fig. 5.6).

The small supernumerary tubercles on the basal segments of the fingers usually are round or subconical; they are not present on the thumb. These tubercules are comparatively large in a few species (e.g., *Gastrotheca carinaceps*, *gracilis*, *longipes*). In contrast, they are minute and few in a small number of species (e.g., *G. espeletia* and *G. ochoai*), restricted to Finger III (*G. ernestoi*) or Fingers III and IV (*G. fulvorufa*), and absent in others (*G. andaquiensis*, *angustifrons*, *fissipes*, *flamma*, *megacephala*, *stictopleura*, and *zeugocystis*).

Nuptial Excrescenses

During the breeding season, adult males of many species of *Gastrotheca* are known to develop a cornified patch on the inner surface of each thumb. This probably occurs in all species, but the absence of known breeding males of some species preludes stating that this character is universal. The nuptial excrescence is brown in nearly all species possessing a pad, but it is black in some specimens of *G. nicefori*, tan in some specimens of *G. riobambae*, and cream in some males of *G. antomia* and *G. phelloderma*.

Webbing between Fingers

In most species of *Gastrotheca* there is no webbing between the fingers, but basal webbing between Fingers II and III and between Fingers III and IV is present in several species (e.g., *G. andaquiensis*, *cornuta*, *pulchra*). More webbing between the outer fingers is evident only in five species: outer fingers about one-fourth webbed in *G. longipes* and *G. walkeri*, one-third webbed in *G. splendens*, and one-half webbed in *G. albolineata* and *G. williamsoni*.

Tarsal Folds

An outer tarsal fold is absent. In many species of *Gastrotheca*, a slightly curved inner tarsal fold extends from the proximal edge of the inner metatarsal tubercle toward the knee. This fold reaches along the full length of the tarsus in some species (e.g., *G. argenteovirens*, *galeata*, *orophylax*), whereas in others it extends for shorter distances: two-thirds (*G. griswoldi*, *monticola*, and *psychrophila*), one-half (*G. excubitor*, *fulvorufa*, and *marsupiata*), and one-fourth (*G. gracilis* and *G. microdiscus*).

Tubercles on the Foot

The foot always bears an inner metatarsal tubercle at the base of Toe I (Fig. 5.4). As seen in plantar view, this tubercle is variable in size and shape. In most species it is elliptical or ovoid, and it is elevated in some species (e.g., *Gastrotheca aureomaculata*, *galeata*, *microdiscus*). The tubercle is visible from above in those species in which the tubercle is large and elongate (e.g., *G. albolineata*, *christiani*, *pachachacae*). The outer metatarsal tubercle lies at the base of Toe V; it is absent in about half of the species. For those in which it is present, the tubercle usually is small and subconical. The subarticular and supernumerary tubercles are like those on the hands, except that the latter are commonly smaller or restricted to the proximal digit of each toe. The supernumerary tubercles are absent in *G. angustifrons*, *ernestoi*, and *williamsoni*, and they are restricted to the outer toes in four Brazilian species: *G. fissipes*, *flamma*, *megacephala*, and *pulchra*.

Webbing between Toes

In discussing webbing on the feet, the toes are numbered in roman numerals (Fig. 5.4). All *Gastrotheca* have some webbing on their feet, although it is restricted to between Toes III–IV in a few species. For example, webbing is basal between Toes III and IV and between Toes IV and V in *G. antomia*, *antoniiochoai*, *fissipes*, *megacephala*, *nebulanastes*, and *ossilaginis*. The least amount of webbing is in *G. zeugocystis*, in which webbing is absent between Toes IV and V.

The extent of webbing between the toes is described in two ways. In the diagnoses, the amount of webbing is noted solely for Toes IV and V, as this is its maximum extent in relation to the subarticular tubercles, the distal one being at the base of the disc; proceeding proximally are the penultimate and antepenultimate tubercles. Although webbing extends to the distal tubercle on Toe V in several species, it reaches the distal tubercles on Toes IV and V in only four species: *Gastrotheca cornuta*, *longipes*, *walkeri*, and *williamsoni*. Herein, a generalized terminology is applied for quick comparisons. If the webbing extends to the distal tubercles, the foot is said to be fully webbed; if it extends to the penultimate tubercles on Toes IV and V, the foot is three-fourths webbed; and if it extends only to the antepenultimate tubercles on those toes, the foot is one-half webbed.

A more concise method is used in the descriptions, wherein the webbing formula defined by Savage and Heyer (1967) and modified by Myers and Duellman (1982) is used. Therein, roman numerals denote the digits and arabic numerals represent the number of phalanges completely or partially free of webbing. The extent of the webbing may be different on each side of a given digit; therefore, the webbing formula notes the extent on both sides. For example, **I**2—3**II**2—2^+**III**1^-—1**IV**1—(2^-—2)**V**.

In this example, webbing extends to the penultimate subarticular tubercle on Toe I and only to the antepenultimate tubercle on Toe II; essentially, this small amount of webbing would be termed basal. On the outer edge of Toe II, the webbing is at the penultimate tubercle and extends slightly beyond the penultimate tubercle on Toe III. On the outer edge of Toe III, the webbing is slightly proximal to the distal tubercle. On both sides of Toe IV, the webbing extends to the distal tubercle. Displaying the extents of the webbing in parentheses denotes a variation in the webbing at a particular place. Thus, in the above formula, the webbing extends to slightly less than or up to the penultimate tubercle.

Skin Texture

The skin the chest and the belly is granular in all hemiphractid frogs. In *Gastrotheca*, the skin on the flanks generally is smooth or areolate (smooth with intervening narrow depressions), but the skin on the dorsal surfaces of the body and the limbs is highly variable. Most commonly, the dorsum is denoted as smooth or finely granular; this also includes scattered tubercles. In a few species (*G. antoniiochoai*, *atympana*, *ossilaginis*, and *stictopleura*), the skin is termed shagreen (sandpaper- or sharkskin-like). In some species, distinctly elevated pustules are evident, especially dorsolaterally on the body and on the dorsal surfaces of the thigh; such pustules are present in *G. marsupiata*, *pacchamama*, *peruana*, *phalarosa*, and *pseustes*. The most pustular dorsal skin is in *G. phelloderma*, in which pustules form longitudinal ridges on the body.

Some species of *Gastrotheca* have ridges on the head

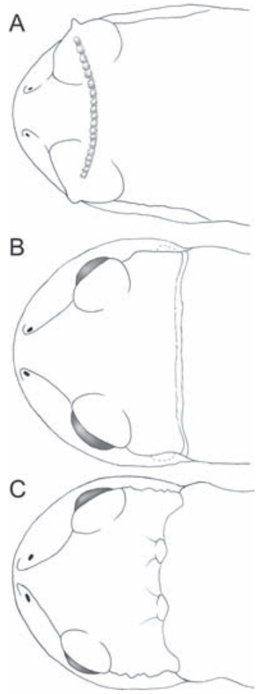

Fig. 5.7 Transverse ridges on the head. A: interocular ridge, *Gastrotheca andaquiensis* (KU 164245). B: smooth occipital ridge, *G. nicefori* (KU 192401). C: occipital ridge with dorsal projections, *G. ovifera* (KU 133388).

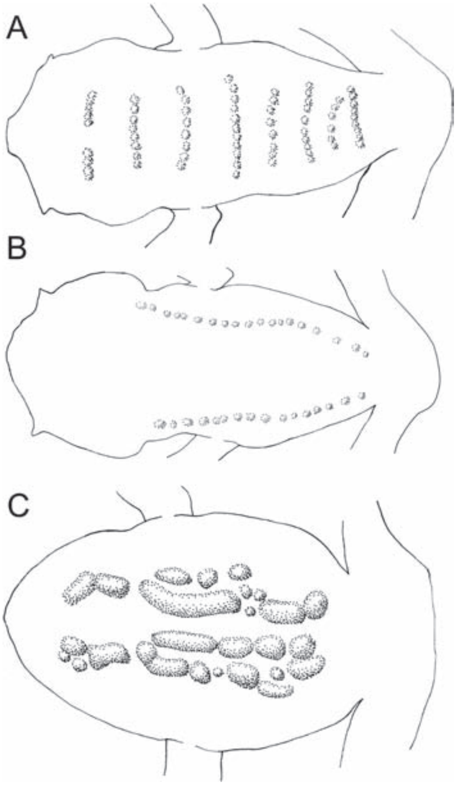

Fig. 5.8 Dorsal body features. A: transverse granular ridges, *Gastrotheca dendronastes* (KU 169394). B: dorsolateral tubercular ridges, *G. bufona* (ICN 38083). C: longitudinal pustular ridges, *G. phelloderma* (KU 331040).

(Fig. 5.7) or the body (Fig. 5.8). A transverse interocular dermal ridge is present in *G. andaquiensis*, whereas a bony transverse occipital ridge is evident in *G. nicefori* and *G. ovifera*. Transverse dermal ridges are present on the dorsal surfaces of the body in *G. angustifrons*, *cornuta*, and *dendronastes*; the ridges are granular in the latter species and smooth in the others. A granular dorsolateral fold is present on the anterior two-thirds of the body in *G. bufona*.

Dermal Ornamentation

All species of *Hemiphractus* have a fleshy proboscis, a feature unknown in other genera in this family. In all species of *Hemiphractus* and some of *Gastrotheca*, a large tubercle or fleshy protrusion (supraciliary process) is present (Fig. 5.9). Eyelid tubercles are present in two Brazilian species: two on each eyelid in *G. flamma*, and one in *G. pulchra*. The process is a small triangle in *G. walkeri*. Most species in the subgenus *Amphignathodon* have distinctive supraciliary processes; these are long in *G. bufona* and *G. guentheri*, and distally bifurcate in the former.

In some species of *Gastrotheca*, the heel is adorned with one (e.g., *G. angustifrons*, *ovifera*, *testudinea*) or two (*G. antomia*) tubercles or a fleshy calcar (Fig. 5.10). The calcar is triangular in *G. cornuta*, *guentheri*, *pacchamama*, *pulchra*, *walkeri*, *weinlandii*, and *williamsoni*. It is elongate and triangular in *G. andaquiensis*, *bufona*, and *flamma*.

The cloacal region also has dermal protrusions. Three species of *Gastrotheca* (*G. albolineata*, *longipes*, and *plumbea*) have a vertical fold of skin on either side of the cloacal opening; the folds are weak in *G. albolineata*. Numerous species have tubercles diverging ventrolaterally from the cloacal opening. Most commonly there is only one pair of tubercles (e.g., *G. cornuta*, *fissipes*, *testudinea*). In those species having more than one pair, the tubercles decrease in size distally. There are three pairs in *G. megacephala* and *G. phelloderma*, and as many as four pairs in *G. fulvorufa*, *guentheri*, and *stictopleura*.

Opening of the Brood Pouch

In females of most species of *Gastrotheca*, the opening of the brood pouch is a relatively small aperture that,

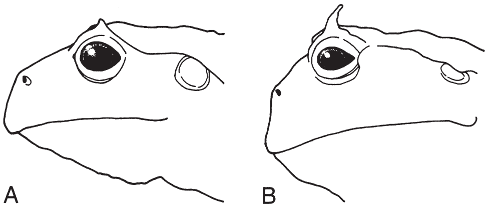

Fig. 5.9 Supracilliary processes. A: triangular, *Gastrotheca walkeri* (KU 166768). B: elongate, *G. guentheri* (KU 164224).

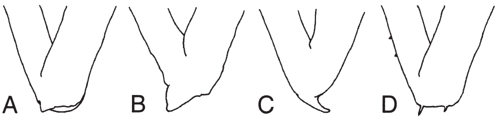

Fig. 5.10 Dorsal views of left heels, showing different shapes of the appendages. A: small triangular calcar, *Gastrotheca dendronastes* (KU 169389). B: large triangular calcar, *G. guentheri* (KU 164224). C: elongate curved calcar, *G. bufona* (ICN 38083). D: pair of elongate tubercles and pair of conical tubercles on the outer edge of the tarsus, *G. antomia* (KU 289244).

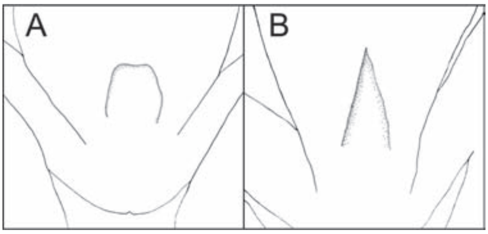

Fig. 5.11 Brood pouch openings. A: U-shaped, *Gastrotheca orophylax*, KU 178583. B: V-shaped, *G. dendronastes*, KU 169394.

together with the dermal ridges posterior to the opening, is U-shaped. The arboreal species that give birth to froglets (e.g., *G. cornuta*, *guentheri*, *longipes*) have a V-shaped opening with longer dermal ridges (Fig. 5.11). In two of these species (*G. antoniiochoai* and *G. zeugocystis*) the pouches diverge laterally, so that they are on the sides of the body. In two others (*G. walkeri* and *G. williamsoni*) the pouches are laterally retroperitoneal.

Coloration

Color Pattern Characters

Fourteen aspects of coloration were coded in a binary fashion and used in the multivariate analyses.

Pale labial stripe. The labial stripe was coded as absent or present and, if present, whether or not it extended onto the flanks.

Pale dorsolateral stripe. This stripe was coded as absent or present.

Dark canthal stripe. This stripe was coded as absent or present.

Pale suborbital bars. These bars were coded as absent or with one, two, or three bars.

Dark interorbital bar. This bar was coded as absent or present.

Dorsal paravertebral marks. At least a part of the pattern on the dorsum of the body in many species of *Gastrotheca* consists of a pair of longitudinal markings (paravertebral marks), which were coded as absent or present.

Dorsal body pattern. Major aspects of the color pattern were coded as follows: (A) dorsum uniform or patterned, and (B) dorsum dark or pale. If the dorsum was patterned, the following pattern elements were coded: (C) dark or pale, (D) mottled, (E) with flecks, (F) with spots, (G) small, (H) large, (I) with a narrow middorsal mark, (J) with a broad middorsal mark, and/or (K) with transverse lines.

Flank pattern. The flanks were coded as (A) uniform or patterned, and (B) dark or pale. If the flanks were patterned, the following pattern elements were coded: (C) dark or pale, (D) with spots, (E) with stripes, (F) with vertical bars, (G) blue with black spots, or (H) with an intrusion of the dorsal pattern.

Dorsal shank pattern. The shanks were coded as (A) uniform or patterned, and (B) pale or dark. If patterned, the pattern elements were coded as (C) dark or pale, (D) with spots, or (E) with transverse bars.

Anterior thigh pattern. This was coded as (A) uniform or patterned, and (B) blue or not. If patterned, the pattern elements were coded as (C) mottled, (D) with dark spots, or (E) with dark vertical bars.

Posterior thigh pattern. This was coded as (A) uniform or patterned, and (B) dark or pale. If patterned, the pattern elements were coded as (C) dark or pale, (D) with spots, or (E) with vertical bars.

Cloacal region pattern. In some species of *Gastrotheca* there is a dark patch in the cloacal region; furthermore, there may be a pale transverse supracloacal stripe and/or one or more pairs of pale spots below the cloacal opening. These were coded as (A) pattern absent or present, (B) with a dark patch, (C) with a stripe, (D) with one pair of spots, or (E) with more than one pair of spots.

Ventral pattern. This was coded as (A) uniform or patterned, and (B) pale or dark. If patterned, the pattern elements were coded as (C) pale or dark, (D) with spots, or (E) with flecks.

Foot color. In some species of *Gastrotheca*, Toes IV and V and the web between those toes is dark, as contrasted with a much paler color of the other toes and webs. The coloration of the toes was coded as (A) uniform or (B) with the outer toes dark.

Other Color Characters

Three other color characters used in the diagnoses and descriptions were not coded in a binary fashion and were not used in any of the analyses herein.

Pale canthal stripe. In some species there is a narrow pale canthal stripe immediately above the dark canthal stripe; in some species this pale canthal stripe is continuous along the outer edge of the eyelid, along with the pale dorsolateral stripe.

Post-tympanic mark. Some species have a broad post-tympanic dark mark.

Tympanum color. The tympanum may be the same color as the surrounding area, or it may be pale in comparison; in some of the latter species, the tympanum is golden or bronze colored in life (e.g., *Gastrotheca aureomaculata*).

Coloration in Life

Descriptions of the colors in live frogs were taken from field notes; these are identified as to collector and date. Also, color photographs were used. In some cases, information has been retrieved from the literature, in which case a reference is given.

Tadpoles

The developmental stages of tadpoles are those defined by Gosner (1960) and illustrated by Duellman and Trueb (1986). All specimens were preserved and stored in 10% buffered formalin. Whenever possible, comparisons were made between tadpoles in the same stage of development. Illustrations of tadpoles and a tabulation of their morphological characters are found in chapter 7.

Measurements

The following measurements were made to the nearest 0.1 mm, using needle-tipped dial calipers.

Total length. The straight-line distance from the tip of the snout to the tip of the tail.

Body length. The straight-line distance from the tip of the snout to the posterior edge of the body, not including the cloacal tube.

Tail length. The total length minus the body length.

Body width. The greatest width of the body.

Body depth. The greatest depth of the body.

Interorbital distance. The distance between the eyes.

Eye diameter. The length of the orbit.

Eye–nostril distance. The distance between the anterior edge of the orbit and the median point of the narial aperture.

Eye–snout distance. The distance between the anterior edge of the orbit and the tip of the snout.

Width of oral disc. The greatest width of the disc, measured from the lateral borders of the labia.

Height of caudal musculature. The height of the musculature at the midlength of the tail.

Height of tail. The height of the tail at its midlength.

External Structural Characters

Many structural characters were recorded and used where appropriate in the descriptions herein.

Snout shape. In dorsal view the snout may be round, or gradually inclined from the nostrils to the tip of the snout.

Body shape. In dorsal view the body is widest at midlength or posteriorly (ovoid), or compressed at midlength (violin-shaped); in profile the throat is convex in most species, but concave in some.

Eye direction. The eyes are directed dorsolaterally in most species, but nearly laterally in some others.

Narial direction. The external nares may be directed anterolaterally, anterodorsally, or dorsolaterally.

Spiracle. The single spiracular tube is sinistral and directed posterodorsally in all species of *Gastrotheca*. Slight interspecific differences occur in the length of the tube; the position of the aperture is designated with respect to the length and depth of the body.

Position of the cloacal tube. The tube may be dextral or sinistral to the ventral caudal fin, or incorporated within it (median).

Shape of the cloacal tube. The tube may be cylindrical and gradually diminishing in diameter distally, or it may be flask-shaped.

Aperture of the cloacal tube. The opening of the cloacal tube is transverse to the longitudinal axis of the cloacal tube in some species; in other species it is diagonal.

Origin of the dorsal caudal fin. The dorsal fin originates gradually in some species, whereas in others it originates abruptly.

Termination of the caudal fin. The caudal fin may terminate distally in a gradually narrowing tip, or it may terminate in a more bluntly rounded tip.

Marginal papillae. The median part of the upper lip is bare, and laterally there is a single row of papillae on the upper lip in all species of *Gastrotheca* having free-living tadpoles. On the lower lip the tubercles may be arranged in a single row, in two parallel rows, or in two alternating rows. In some species the condition differs midventrally from the lateral arrangement on the lower lip. The papillae vary from blunt to acuminate.

Labial teeth. All tadpoles of *Gastrotheca* have two upper and three lower rows of denticles; the second upper row is always interrupted medially. Interspecific differences exist in the relative lengths of the rows.

Jaw sheaths. The lower sheath in all species is moderately massive and broadly V-shaped. Interspecific differences exist in the relative size and shape of the serrations on the sheaths and in the shape of the upper sheath, which may be in the form of a continuous arch (sigmoid).

Coloration. Tadpoles of *Gastrotheca* lack distinctive colors and patterns. Their coloration is described from preserved specimens and from field notes made on living individuals.

Larval Buccal Morphology

Tadpoles of eight species were dissected and stained following the procedures given by Wassersug (1976) and prepared for scanning electron microscopy in the manner described by Wassersug and Rosenberg (1979). All preparations were done by Richard J. Wassersug, who examined and photographed the specimens on a Cambridge Stereoscan electron microscope. The descriptions were presented by Wassersug and Duellman (1984). Although some quantifiable differences in buccal features exist among the tadpoles of *Gastrotheca* that were studied, variation in all of those characters is found within large samples of a single species, so none is considered to be significant systematically.

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6

Chromosomes, Muscles, and Vocalization

In addition to the osteological and external morphological characters discussed in chapters 4 and 5, other features have been used in the systematics of hemiphractid frogs. Some of these are definitely useful in distinguishing species, and others have at least a limited utility in the interpretation of phylogenetic relationships. Some other features, especially the muscles and tendons of the hands and feet (Andersen, 1978; Burton, 1998), as well as the eye and jaw musculature (da Silva, 1998), are not included, because the states of the characters are known in so few hemiphractid frogs.

Chromosomes

The first rather primitive descriptions of chromosomes of hemiphractid frogs were of *Gastrotheca cornuta* by Duellman (1967) and of *Fritziana goeldii* by Beçak (1968). These were followed by detailed descriptions of the chromosomes of *G. gracilis* and the three then-recognized species of *Fritziana* by Bogart (1973). Karyological studies of hemiphractids languished until Schmid et al. (1983a, 1983b) used newly developed banding techniques to discover the sex chromosomes in *G. riobambae*. These seminal publications were followed by numerous papers on chromosome banding and sex chromosomes in *Gastrotheca* (e.g., Schmid et al., 1988, 1990). Schmid's intensive work on hemiphractids, including cytogenetic data from 397 specimens of 23 species, culminated in a detailed and thoroughly illustrated volume (Schmid et al., 2013).

Fieldwork in Brazil in 1986 and Venezuela in 1987 by Michael Schmid and his associates resulted in the collection of specimens of *Gastrotheca "fissipes"* [= *G. megacephala*] in Brazil and of *Flectonotus pygmaeus*, *G. ovifera*, and *G. walkeri* in Venezuela. The karyological data obtained through the preparations from these species and from that of an earlier study (Schmid et al., 1983a) on *G. riobambae* led to the first comparative study of *Gastrotheca* chromosomes (Schmid et al., 1988). Therein, the authors demonstrated that the diploid number of chromosomes ($2n = 26$) reported for *G. gracilis* by Bogart (1973) seemed to be universal in *Gastro-*

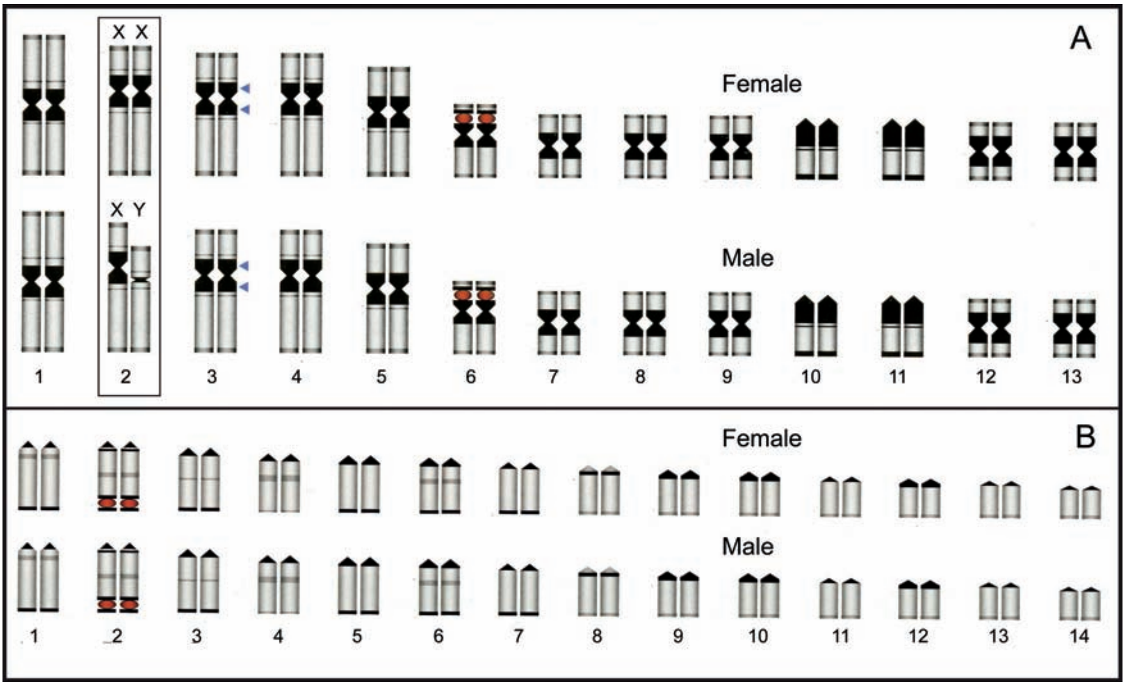

Fig. 6.1 Idiograms of female and male karyotypes of two species of hemiphractid frogs. A: *Gastrotheca walkeri* (2*n* = 26). B: *Flectonotus pygmaeus* (2*n* = 28). Chromosomes display C-banding of the constitutive heterochromatin (black), Ag-staining of the nucleolus organizer regions (red), and the size heteromorphisms (blue). The sex chromosomes of *G. walkeri* are enclosed in a box. Adapted from Schmid et al. (2013).

theca, They suggested that the haploid number of 14, based on the testicular squash technique (Duellman, 1967), probably consisted of 12 autosomal bivalent chromosomes plus 1 XY bivalent chromosome.

The chromosomes of hemiphractid frogs usually are metacentric, but they are telocentric in *Flectonotus*, which has 28 chromosomes (Fig. 6.1). The diploid number of chromosomes apparently is 26 in all specimens of *Cryptobatrachus*, *Gastrotheca*, and *Stefania* that have been studied, and it is unknown in *Hemiphractus* (Table 6.1). In those species having a diploid number of 26, there are 5 pairs of large chromosomes and 8 pairs of small chromosomes, whereas in *Flectonotus*, all chromosomes are approximately the same size.

Bogart (1973) clearly showed that each of the three species of *Fritziana* then recognized had different chromosome complements. The karyotype of *F. goeldii* is essentially like that of *Gastrotheca*, with 5 pairs of large metacentric and submetacentic chromosomes and 8 pairs of small metacentric, submetacentric, or telocentric chromosomes. *F. ohausi* has 4 pairs of large metacentric and submetacentric chromosomes and 10 pairs of small mostly submetacentric and telocentric chro-

Table 6.1 Diploid (2*n*) and fundamental (FN) numbers of chromosomes in 19 species of hemiphractid frogs

Species	2*n*	FN
Cryptobatrachus boulengeri	26	52
Flectonotus fitzgeraldi	28	28
Flectonotus pygmaeus	28	28
Fritziana fissilis	30	50
Fritziana goeldii	26	42
Fritziana ohausi	28	44
Gastrotheca andaquiensis	26	46
Gastrotheca espeletia	26	44
Gastrotheca gracilis	26	52
Gastrotheca griswoldi	26	52
Gastrotheca megacephala	26	52
Gastrotheca monticola	26	52
Gastrotheca nicefori	26	50
Gastrotheca ovifera	26	52
Gastrotheca peruana	26	50
Gastrotheca pseustes	26	52
Gastrotheca riobambae	26	38
Gastrotheca walkeri	26	38
Stefania scalae	26	52

mosomes, thereby giving this species a chromosome complement of $2n = 28$. *F. fissilis* has a complement of $2n = 30$, consisting of 4 pairs of large metacentric or submetacentric chromosomes and 11 pairs of small chromosomes having a variety of centromere positions. So far as is known, *Fritziana* is the only genus of hemiphractid frogs having interspecific differences in the number of chromosomes.

Aside from slight differences in the sizes of the chromosomes, their banding patterns, and the positions and quantities of their constitutive heterochromatin, the few species of hemiphractids studied reveal differences in the nucleolus organizing regions (NORs). Positions of the NORs are given in relation to the centromeric and telocentric regions, and the chromosome arms are divided into centroimeric, medial, and telomeric regions. Of the 24 species for which NOR positions were determined, 16 were centromeric and 8 were telomeric (Schmid et al., 2013).

Supernumerary chromosomes are rare among frogs; according to Schmid et al. (2013), they are known in only 14 species of anurans. *Gastrotheca espeletia* is the only hemiphractid frog known to have supernumerary chromosomes, which are smaller than the regular chromosomes. Forty-nine individuals of *G. espeletia* had one to nine supernumerary chromosomes.

The sex chromosomes (XY in males, and XX in females) are highly differentiated. In contrast to all other known amphibian karyotypes, the autosomes and X chromosomes contain large amounts of constitutive heterocromatin, and there is very little heterochromatin in the Y chromosome. Schmid et al. (1990) reported that *Gastrotheca pseustes* had two types of Y chromosomes and hypervariability in their heterochromatin.

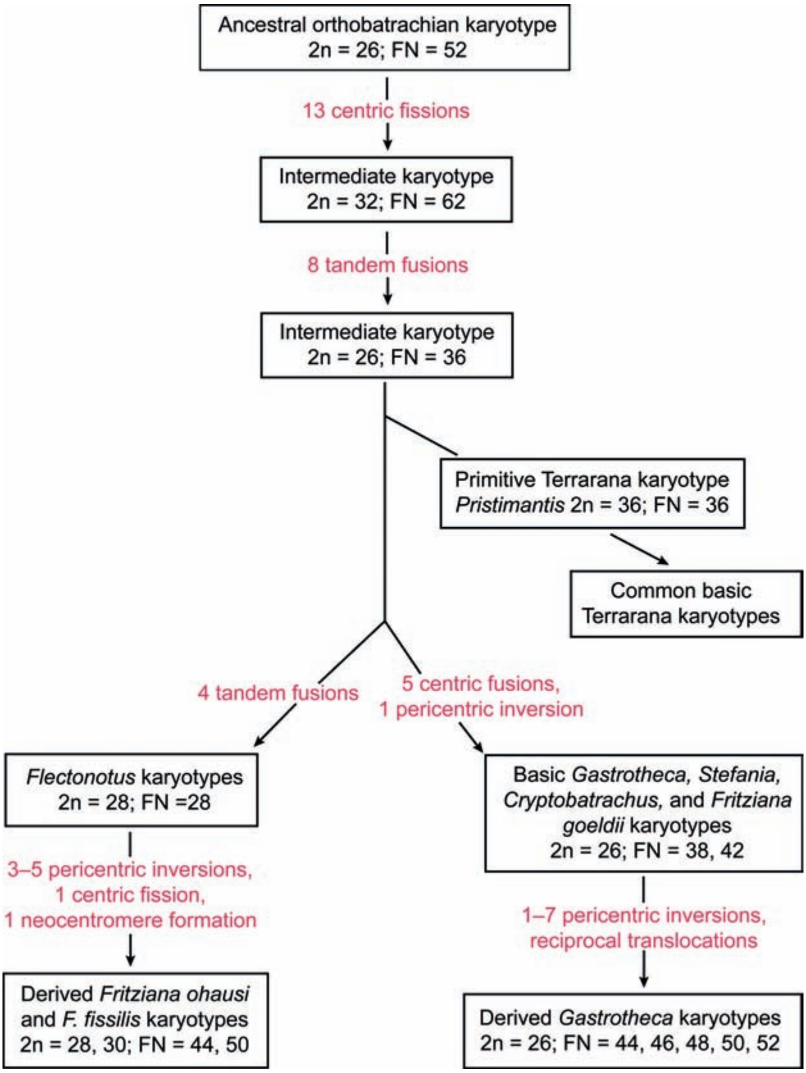
Ancestral orthobatrachian karyotype
2n = 26; FN = 52
13 centric fissions
Intermediate karyotype
2n = 32; FN = 62
8 tandem fusions
Intermediate karyotype
2n = 26; FN = 36
Primitive Terrarana karyotype
Pristimantis 2n = 36; FN = 36
Common basic Terrarana karyotypes
4 tandem fusions
5 centric fusions, 1 pericentric inversion
Flectonotus karyotypes
2n = 28; FN =28
Basic Gastrotheca, Stefania, Cryptobatrachus, and Fritziana goeldii karyotypes
2n = 26; FN = 38, 42
3–5 pericentric inversions, 1 centric fission, 1 neocentromere formation
1–7 pericentric inversions, reciprocal translocations
Derived Fritziana ohausi and F. fissilis karyotypes
2n = 28, 30; FN = 44, 50
Derived Gastrotheca karyotypes
2n = 26; FN = 44, 46, 48, 50, 52

Fig. 6.2 Theoretical phylogeny of karyotypes of hemiphractid frogs. Schmid et al. (2013).

Inasmuch as the Y chromosomes of some specimens were homomorphic and others heteromorphic, the authors intimated that they possibly were dealing with more than one species. Unfortunately, the specimens were purchased from an animal dealer who stated that the 98 frogs came from Provincia de Loja in southern Ecuador, but some specimens subsequently were identified as *G. riobambae*, which does not occur in that part of the country. No voucher specimens exist, but the karyological data may refer to *G. lojana* as well as to *G. pseustes*.

Sex chromosomes have been determined for five species of *Gastrotheca* (*G. ovifera*, *peruana*, *pseustes*, *riobambae*, and *walkeri*). In all of these the system is XX/XY. In *G. peruana* and *G. pseustes*, the chromosomes are nearly the same size but differ in their replication banding patterns, centromeric index, amount of constitutive heterochromatin, the presence of an NOR in only one of the two sex chromosomes, or the involvement of the Y chromosome in a centric fusion with an autosome. In *G. ovifera* and *G. walkeri* the X chromosome is larger than the Y chromosome, whereas the reverse exists in *G. riobambae* (Schmid et al., 2013).

An elaborate diagram showing a theoretical karyophylogeny of hemiphractid frogs proposed by Schmid et al. (2013:310) includes numerous centric and tandem fusions, followed by pericentric inversions to derived karyotypes of *Gastrotheca*, *Flectonotus*, and *Fritziana* from an "ancestral orthobatrachuan" karyotype (Fig. 6.2). An alternative theoretical karyophylogeny on the facing page includes early pericentric inversions, followed by many centric and tandem fusions. In both "phylogenies" *Fritziana* and *Flectonotus* are "derived" genera, inasmuch as the former has 13, 14, or 15 pairs of chromosomes and the later has 14 pairs of telocentric chromosomes.

Neither of these theoretical phylogenies of hemiphractid karyotypes is like the phylogeny based on molecular data (Fig. 3.1), in which *Flectonotus* is the sister taxon of *Cryptobatrachus* in the most basal clade of hemiphractids. Likewise, *Fritziana* also is among the basal taxa of hemiphractids, whereas *Gastrotheca* is the most-derived genus. This arrangement is strongly supported by differences in reproductive behavior and embryonic development (chapter 7). Therefore, the limited data on karyotypes do not reflect the hypothesized phylogenetic relationships among hemiphractid frogs.

Throat Musculature

In a seminal paper, Tyler (1971) demonstrated that differences in superficial throat musculature were correlated with the geographic distribution of species of "*Hyla*." In his broad coverage of New World hylid frogs, he noted differences among the genera now placed in Hemiphractidae. Subsequently, Tyler and Duellman (1995) reported on the superficial throat musculature and vocal sac aperture in 58 species of hemiphractids. Figure 6.3 shows the patterns of the superficial mandibular musculature in hemiphractids, using data from Tyler and Duellman's study together with the results of my examination of additional species.

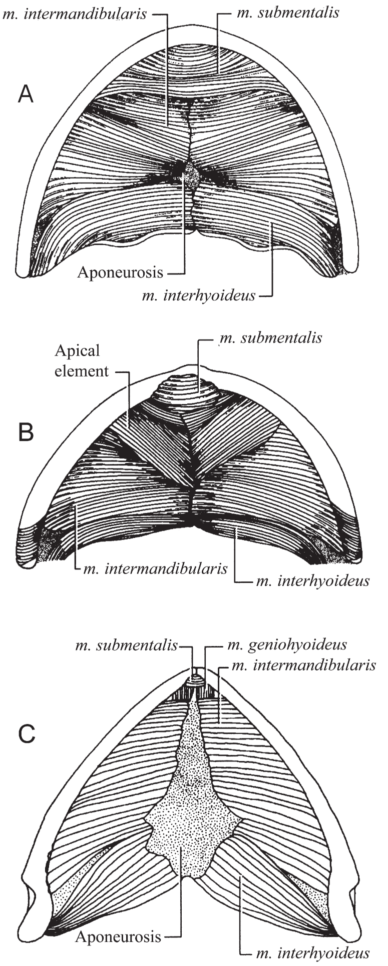

Fig. 6.3 Ventral views of throats, showing the superficial mandibular musculature in hemiphractid frogs. Pattern A: *Gastrotheca dendronastes* (KU 169387), width = 26 mm. Pattern B: *G. dunni* (KU 204114), width = 16 mm. Pattern C: *Hemiphractus fasciatus* (KU 107408), width = 22 mm. Adapted from Tyler and Duellman (1995).

Pattern A: The m. submentalis is moderate in size. The m. intermandibularis is an undifferentiated sheet having a median raphe, and the m. interhyoideus extends posterior to the mandibles.

Pattern B: The m. submentalis is moderate in size. The m. intermandibularis is differentiated, in that it has an apical element, the fibers of which are in contact medially. The m. interhyoideus extends slightly posterior to the mandibles.

Pattern C: The m. submentalis is small. The m. intermandibularis is differentiated, in that it has a large median aponeurosis. The m. interhyoideus does not extend posterior to the mandibles.

Pattern A was discerned in *Flectonotus*, *Fritziana*, *Stefania ginesi*, and some species of *Gastrotheca* (Table 6.2). Pattern B was observed in *Cryptobatrachus fuhrmanni*, two species of *Stefania*, and many species of *Gastrotheca*. Pattern C was found only in the species of *Hemiphractus*.

The vocal apertures are openings in the floor of the mouth in adult males; the openings extend through the m. intermandibularis to the vocal sac. Apertures are absent in *Cryptobatrachus*, *Hemiphractus*, and *Stefania*, all of which apparently are voiceless. Vocal apertures also are absent in various species of *Gastrotheca*, some of which (e.g., *G. albolineata*, *cornuta*, *microdiscus*) are known to have an advertisement call. The apertures are gaping holes in *Flectonotus*, *Fritziana*, and some species of *Gastrotheca*, whereas they are slit-like openings extending posterolaterally from the base of the tongue in other species of *Gastrotheca*, and simply a small orifice in *G. trachyceps* (Table 6.2 and Fig. 6.4).

Within *Gastrotheca*, there is some phylogenetic significance in the patterns of the superficial mandibular musculature. Most of the basal subgenera have Pattern A, but subgenera *Cryptotheca* and *Opisthodelphys* and one species of subgenus *Amphignathodon* (*G. helenae*) have Pattern B, the pattern exhibited by most of the members of subgenera *Duellmania* and *Gastrotheca*. The exception, *G. helenae*, also is the only member of the subgenus *Amphignathodon* with a vocal aperture that is a gaping hole; all the rest have a slit-like aperture or no aperture at all. The only non-*Amphignathodon*

Table 6.2 Mandibular musculature and vocal sac structure among species in the subgenera of *Gastrotheca* (updated from Tyler and Duellman, 1995). Muscle patterns A and B are identified in the text. Vocal sac apertures: GH = gaping hole; S = slit; SO = small orifice; — = absent.

Species	Muscle pattern	Vocal sac aperture
subgenus *Eotheca*		
G. megacephala	A	GH
G. prasina	A	GH
G. recava	A	GH
subgenus *Cryptotheca*		
G. walkeri	B	GH
G. williamsoni	B	?
subgenus *Amphignathodon*		
G. andaquiensis	A	—
G. angustifrons	A	S
G. bufona	A	S
G. cornuta	A	—
G. dendronastes	A	—
G. guentheri	A	S
G. helenae	B	GH
G. longipes	A	—
G. weinlandii	A	S
subgenus *Australotheca*		
G. albolineata	A	—
G. microdiscus	A	—
subgenus *Opisthodelphys*		
G. ovifera	B	GH
subgenus *Edahotheca*		
G. galeata	A	GH
subgenus *Duellmania*		
G. argenteovirens	B	GH
G. aureomaculata	B	GH
G. dunni	B	GH
G. espeletia	B	S
G. lojana	A	GH
G. monticola	A	GH
G. nicefori	A	GH
G. orophylax	B	GH
G. plumbea	B	GH
G. riobambae	B	GH
G. ruizi	B	GH
G. trachyceps	B	SO
subgenus *Gastrotheca*		
G. abdita	B	GH
G. atympana	B	—
G. aratia	B	GH
G. christiani	B	GH
G. chrysosticta	B	GH
G. excubitor	B	GH
G. gracilis	B	GH
G. griswoldi	B	GH
G. lateonota	B	GH
G. marsupiata	B	GH
G. nebulanastes	B	GH
G. ochoai	B	GH
G. pacchamama	B	GH
G. peruana	B	GH
G. phalarosa	B	GB
G. pseustes	A	GH
G. psychrophila	B	GH
G. rebeccae	B	GH
G. testudinea	B	—

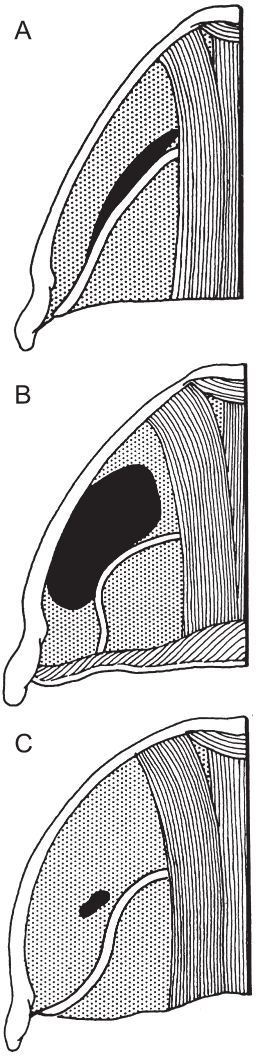

Fig. 6.4 Ventral views of throats, showing the kinds of vocal sac apertures in hemiphractid frogs. A: slit. B: gaping hole. C: small orifice. Tyler and Duellman (1995).

member of the genus that has a slit-like aperture is *G. espeletia*. Thus, within *Gastrotheca*, Pattern B appears to be the derived condition. Within the family, Pattern A is widespread in the basal genera, but the one *Cryptobatrachus* species that was examined has Pattern B.

Vocalization

Males of most anurans produce sounds that have been defined as follows: advertisement calls to attract mates, territorial calls in response to calls by another individual, encounter calls evoked during close-range agonistic interactions, and distress calls when either sex is disturbed (Duellman and Trueb, 1986). Vocal slits and vocal sacs are absent in *Cryptobatrachus*, *Hemiphractus*, and *Stefania*. Males of *Cryptobatrachus* and *Hemiphractus* are not known to call, but the calls of two species of *Stefania* have been recorded (Mägdefrau, 1991; Sinsch and Juraske, 2006d). As noted in the previous section, vocal slits are absent in some species of *Gastrotheca*, some of which (e.g., *G. albolineata*, *cornuta*, *microdiscus*) nonetheless are known to vocalize. Thus the absence of vocal slits and an obvious vocal sac does not preclude vocalization.

I personally have made only a few recordings of *Gastrotheca*, so the following summary of vocal behavior in hemiphractid frogs has been drawn from the published works of numerous persons who have recorded these frogs in the field or the laboratory. The first detailed descriptions of advertisement calls of hemiphractids were those by Duellman (1970) of *G. cornuta* and *G. nicefori* from Panama. Sinsch and Joermann (1989) provided the first indication of "aggressive" (= territorial) calls by a hemiphractid frog. They showed that the advertisement call of *G. marsupiata* consisted of a long pulsed note, whereas the territorial call was a long pulsed note followed by two or more short single-pulsed notes.

Duellman and Gray (1983) and Sinsch and Juraske (2006c) described the calls of *Flectonotus* and *Fritziana*. The call of *Fl. pygmaeus* consists of a single note that resembles a short buzz; it has a dominant frequency of 1600–1800 Hz ($\bar{x} = 1740$). The call of *Fl. fitzgeraldi* has 3–5 notes ($\bar{x} = 4.5$) and a slightly higher dominant frequency of 2400 Hz (Fig. 6.5A and B). In comparison with *Flectonotus*, the calls of *Fritziana* have higher dominant frequencies (2400–3400 Hz) and more notes per call group (Fig. 6.5C): 2 in *Fr. fissilis*, 4–5 in *Fr. goeldii*, and 5–8 in *Fr. ohausi* (Duellman and Gray, 1983).

According to Sinsch and Juraske (2006d:160), the calls of "*Stefania evansi*" [= *S. scalae*] and *S. riveroi* "resemble a faint, hoarse dog barking due to their relative low dominant frequency and tonal call structure." The call of *S. scalae* consists of one or two notes (Fig. 6.6); in the latter the second note is louder and slightly longer (111 milliseconds) than the first (128 milliseconds). Both have a similar dominant frequency (1050 and 980 Hz). In the call of *S. riveroi* the mean duration of the single note is 256 milliseconds, and the mean dominant frequency is 860 Hz. Less than 10% of the calls have a secondary note that is shorter (mean = 147 milliseconds) and a slightly lower dominant frequency (780 Hz).

Distinct interspecific differences exist in the calls of species of *Gastrotheca*. These differences are mainly in the pulse structure, duration, and repetition rate of

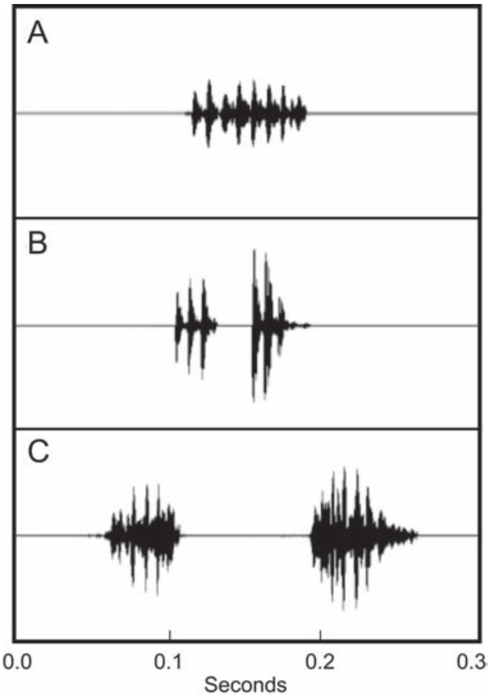

Fig. 6.5 Oscillograms of calls of *Flectonotus* and *Fritziana*. A: *Fl. pygmaeus*, recorded at Rancho Grande, Aragua, Venezuela, 20°C. B: *Fl. fitzgeraldi*, recorded at Simla Tropical Research Station, Trinidad, 20.2°C. C: *Fr. goeldii*, recorded at São Conrado, Rio de Janeiro, Brazil, 22.4°C. A from Duellman and Gray (1983); B and C from Sinsch and Juraske (2006c).

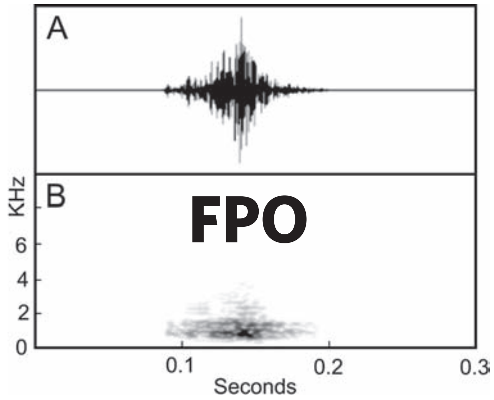

Fig. 6.6 Single-note call of *Stefania scalae*, recorded in captivity, of a male from La Escalera, Bolívar, Venezuela, recorded at 22.6°C. A: oscillogram. B: spectrogram. Sinsch and Juraske (2006d).

the notes. Temperature influences various aspects of the calls, especially in the Andes, where temperature changes are extreme and rapid. I encountered *G. marsupiata* calling at 0°C, and Esteban Lavilla (pers. comm.) observed *G. christiani* calling at −4°C, but these species usually are calling at temperatures of 15°C–20°C. Sinsch (1988) provided the first informative data on the influence of temperature on the calling of a marsupial frog. Analyses of calls of captive individuals at temperatures of 7°C–20°C revealed that the note-repetition rate increased and the duration of the notes decreased with increasing temperature, yet the dominant frequency remained about the same. The calls of *Gastrotheca* generally have low fundamental and dominant frequencies. In nearly all species the dominant frequency is less than 2000 Hz, and even less than 1000 Hz in *G. cornuta* and *G. nicefori*. But in a few species it is higher; the highest reported dominant frequency ($\bar{x}$ = 2915 Hz) is that of *G. antoniiochoai* (Catenazzi and von May, 2011).

Some of the arboreal species in the lowlands and forested slopes of the mountains adjacent to the Andes have calls that may contain one note or a series of notes that are alike in their frequency and structure. *Gastrotheca cornuta* most frequently produces single notes several minutes apart, but then may produce 2–4 notes in quick succession. This same kind of call is produced by *G. guentheri*, whereas the call of *G. albolineata* consists of 5–14 short notes (Fig. 6.7). Three species of Andean frogs (*G. helenae*, *orophylax*, and *plumbea*) also produce series of short notes (Fig. 6.8C).

Throughout the species accounts in chapters 10 and 12, calls are described as consisting of a single long note (Fig. 6.8A) or as a long note followed by two or more short notes (Fig. 6.8B). These secondary notes have the same frequencies but fewer pulses than the primary notes. *Gastrotheca piperata* is an exception, producing a single secondary note that has only one pulse (Fig. 6.8D).

By means of their many observations in the field and experiments in the laboratory, Sinsch and Joermann (1989) showed that in *Gastrotheca marsupiata*, the

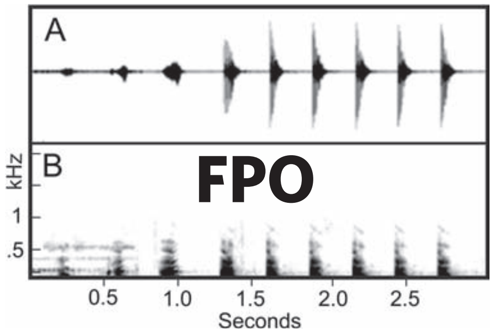

Fig. 6.7 Call of *Gastrotheca albolineata*, recorded at Serra dos Orgãos, Rio de Janeiro, Brazil. A: oscillogram. B: spectrogram. Adapted from Izechsohn and Carvalho-e-Silva (2008).

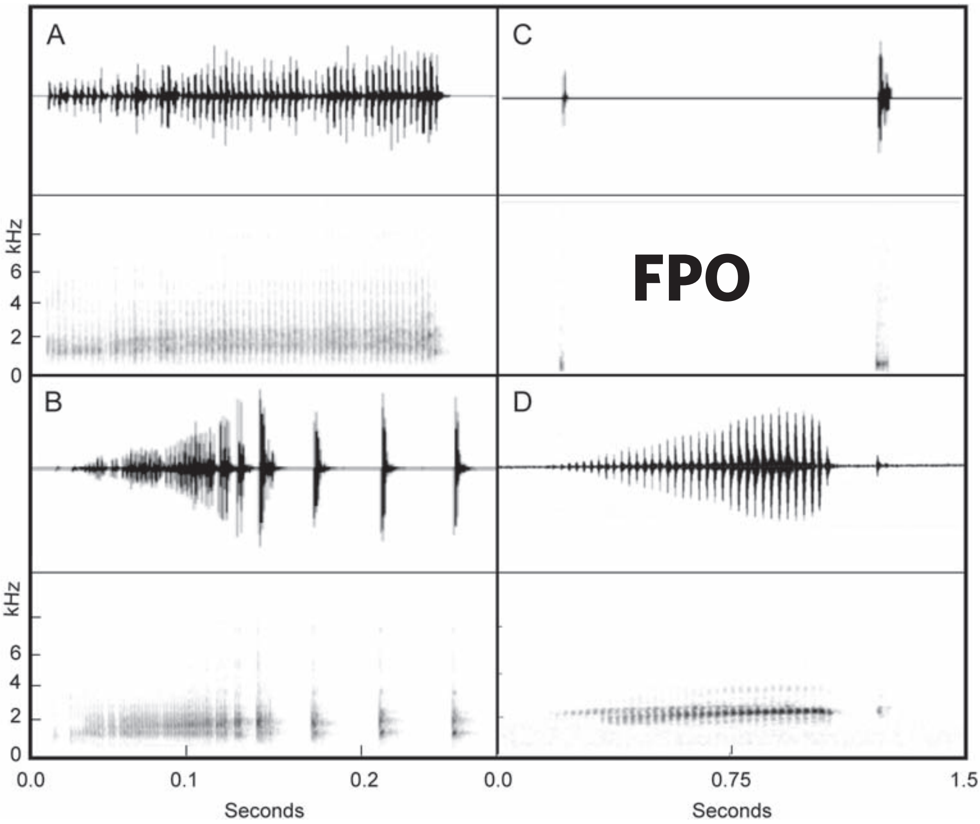

Fig. 6.8 Oscillograms (*upper portions*) and spectrograms (*lower portions*) of four species of *Gastrotheca*. A: *G. griswoldi*, from Tarma, Junín, Peru, recorded at 7.4°C. B: *G. riobambae* from Chambo-Riobamba, Chimborazo, Ecuador, recorded at 20.0°C. C: *G. orophylax* from San Gabriel, Carchí, Ecuador, recorded at 12.5°C. D: *G. piperata* from Karahuasi, Cochabamba, Bolivia, recorded at 16.6°C. A–C adapted from Sinsch and Juraske (2006a, 2006b); D adapted from Duellman and Köhler (2005).

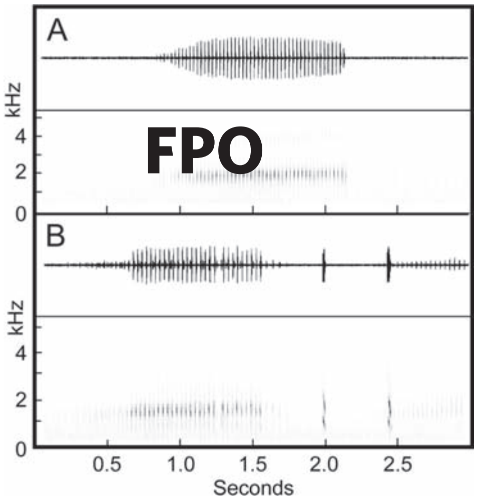

Fig. 6.9 Oscillograms (*upper portions*) and spectrograms (*lower portions*) of *Gastrotheca christiani*. A: advertisement call, recorded at Abra Colorado, Jujuy, Argentina, 11.5°C. B: territorial call, same locality, 18.0°C. Adapted from Viara et al. (2011).

long primary note is the advertisement call. If a calling male hears the advertisement call of another individual, he will add the short notes, thereby producing a territorial call. Thus descriptions of calls consisting of a primary note followed by a series of short notes most likely are territorial calls. This has been demonstrated in only a few species in the field; probably the best is that of *G. christiani* (Fig. 6.9).

A long pulsed primary note seems to be characteristic of members of the Andean subgenera *Gastrotheca* and *Duellmania* (except *G. orophylax* and *G. plumbea*). In most descriptions of calls of Andean species, a long primary note is followed by a series of shorter secondary notes. This same kind of call is characteristic of some members of the subgenus *Amphignathodon*; a long secondary note followed by a series of shorter secondary notes has been noted in *G. andaquiensis*, *dendronastes*, and *weinlandii*. The calls of most Brazilian species consist of two pulsed notes, with the second note usually slightly shorter than the first one, but *G. recava* produces only one note. The limited amount of data on vocalizations of hemiphractid frogs precludes the possible significance of calls with respect to phylogenetic relationships.

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7

Reproductive Biology

The reproductive biology of hemiphractid frogs is unique among the more than 6000 known species of frogs, and it has evolved through changes in their development, morphology, physiology, and behavior. These interrelated modifications are discussed here within the phylogenetic framework of hemiphractids that is based on molecular data (Fig. 7.1). Throughout this account I refer to three kinds of reproduction, resulting in (1) free-living feeding tadpoles, (2) non-feeding tadpoles, and (3) direct development of eggs into froglets. The last two fall into the endotrophic category of Altig and Johnston (1989), but I do not use their terms for guilds. Also, throughout I use the staging table created by Gosner (1960) in preference to the staging table for *Gastrotheca riobambae* (del Pino and Escobar, 1981).

In the mid-1850s, a German morphologist and developmental biologist, David F. Weinland (Fig. 7.2), made some significant discoveries: the egg tooth in reptiles and the nature of the dorsal pouch in *Gastrotheca*. He described and illustrated the bell-shaped gills and gill stalks of an advanced embryo from a female *G. ovifera* (Weinland, 1854). Subsequently, the presence of developing embryos on the dorsum or in a brood pouch was noted in several subsequent descriptions. Noble (1917) reported the same embryonic features in *Hyloscirtus* [= *Cryptobatrachus*] *fuhrmanni* and *Cerathyla* [= *Hemiphractus*] *johnsoni*. The first photographic documentation of birth was again in *G. ovifera*, by Beebe (1946). Most early developmental data have emerged from the extensive research by Eugenia del Pino on *G. riobambae* (del Pino and Escobar, 1981), along with a limited amount of data on *Flectonotus pygmaeus* (del Pino and Humphries, 1978; Macgregor and del Pino, 1982). Some data on early development exist for a few other taxa of hemiphractid frogs (Elinson et al., 1990). Embryogenesis in hemiphractid frogs was summarized by del Pino in Schmid et al. (2012).

Direct development of eggs into froglets has evolved independently many times in diverse groups of anurans, ranging from the aquatic *Pipa* (Pipidae) in South America (Rabb and Snedigar, 1960) to several groups of terrestrial and arboreal frogs. These include entire families and subfamilies: Arthroleptidae in tropical sub-Saharan Africa (Blackburn, 2008),

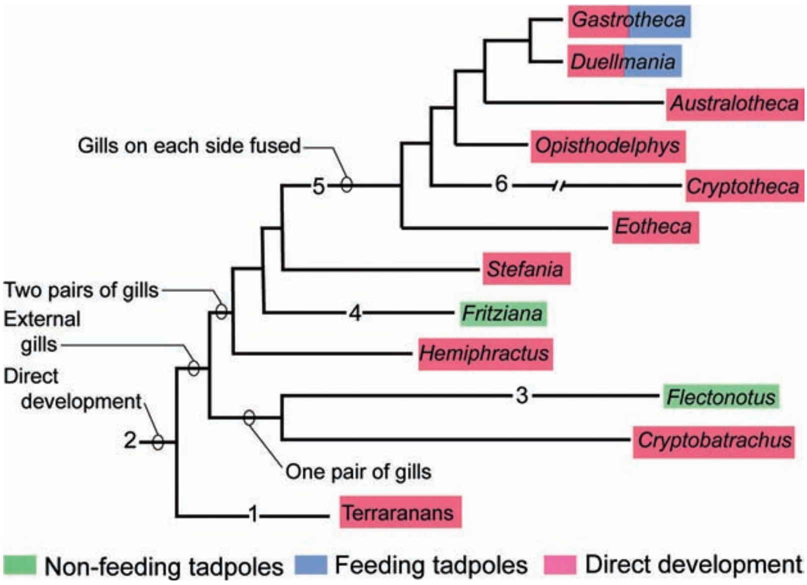
Gastrotheca
Duellmania
Australotheca
Opisthodelphys
Cryptotheca
Eotheca
Stefania
Fritziana
Hemiphractus
Flectonotus
Cryptobatrachus
Terraranans
Gills on each side fused
Two pairs of gills
External gills
Direct development
One pair of gills
1
2
3
4
5
6
🟩 Non-feeding tadpoles
🟦 Feeding tadpoles
🟥 Direct development

Fig. 7.1 Phylogenetic tree of the genera and subgenera of hemiphractid frogs, showing the developmental mode, nature of the external gills, pouch structure, and site of egg development. 1 = eggs on a terrestrial or arboreal surface; 2 = eggs on the dorsum of a female; 3 = eggs in a slit-like pouch; 4 = eggs in a shallow basin; 5 = eggs in a closed pouch; 6 = eggs in a retroperitoneal pouch.

Fig. 7.2 David F. Weinland. Ernst Mayr Library, Museum of Comparative Zoology, Harvard University; courtesy of K. Adler.

Ceratobatrachidae in insular Southeast Asia (Alcala, 1962; Narayan et al., 2011), and Asterophryinae in the Papuan region (Bickford, 2004). Genera characterized by direct development are *Philautus* and *Pseudophilautus* (Rhacophoridae) in India and Sri Lanka (Bossuyt and Dubois, 2001; J-t. Li et al., 2009), *Breviceps* (Brevicepidae) in sub-Saharan Africa (Channing, 2001), *Arthroleptella* (Pyxicephalidae) in southern Africa (Channing, 2001), and *Gephyromantis* (Mantellidae) in Madagascar (Glaw and Vences, 2007). Others are represented by individual terrestrial and fossorial species scattered around the world: *Sooglossus gardineri* (Sooglossidae) in the Seychelles (Nussbaum and Wu, 2007), *Arenophryne rotuda* and *Myobatrachus gouldii* (Myobatrachidae) in western Australia (Roberts, 1981, 1984), and the minute South American microhylid *Myersiella subnigra* (Izecksohn et al., 1971). Combined, there are more than 1200 species in nine families; this clearly demonstrates that direct development has evolved independently in diverse lineages of anurans.

Yet the families and genera noted above actually represent far less than half of the species of frogs that have, or are presumed to have, direct development. Most occur in the American tropics, where the frogs formerly recognized as *Eleutherodactylus* (now five families—Brachycephalidae, Ceuthomantidae, Craugastoridae, Eleutherodactylidae, and Strabomantidae—recognized by Heinicke et al. [2009]) have direct development. This huge array contains nearly 1000 species. The sister-group of these families, termed Terrarana by Hedges et al. (2008) is Hemiphractidae, within which the genera *Cryptobatrachus* (6 species), *Hemiphractus* (6 species), *Stefania* (19 species), and 43 species of *Gastrotheca* have direct development. Although detailed observations on most aspects of the reproductive biology of hemiphractid frogs are woefully incomplete, existing information does provide insights into the reproductive aspects of hemiphractids in an evolutionary framework.

Mating and Oviposition

Male *Flectonotus*, *Fritziana*, and *Gastrotheca* have vocal slits and a distensible vocal sac; during the breeding season, males call to attract females and establish an acoustic territory. *Cryptobatrachus* and *Hemiphractus* lack vocal slits and a vocal sac; they have not been heard to vocalize. *Stefania* resembles those two genera in lacking vocal slits and a vocal sac, but two species are known to call: *S. riveroi* and *S. scalae* (as *S. evansi*) (Mägdefrau, 1991; Sinsch and Juraske, 2006).

Amplexus is thought to be axillary in all hemiphractids, but actual mating has not been observed in *Cryptobatrachus* and *Hemiphractus*. In fact, detailed observations are known for only seven species: Duellman and Maness (1980) and Duellman et al. (2011) for *Flectonotus pygmaeus*; Weygoldt and Carvalho-e-Silva (1991) and Duellman et al. (2011) for *Fritziana goeldii*; Mertens (1957) for *Gastrotheca ovifera*; Auber-Thomay et al. (1990) for *G. plumbea*; Hoogmoed (1967) for *G. riobambae*; Means et al. (2008) for *Stefania ayangannae*; and Mägdefrau (1991) for *Stefania* cf. *riveroi*. Mating takes place in terrestrial habitats, where two behaviors unique to hemiphractids occur; males deposit sperm

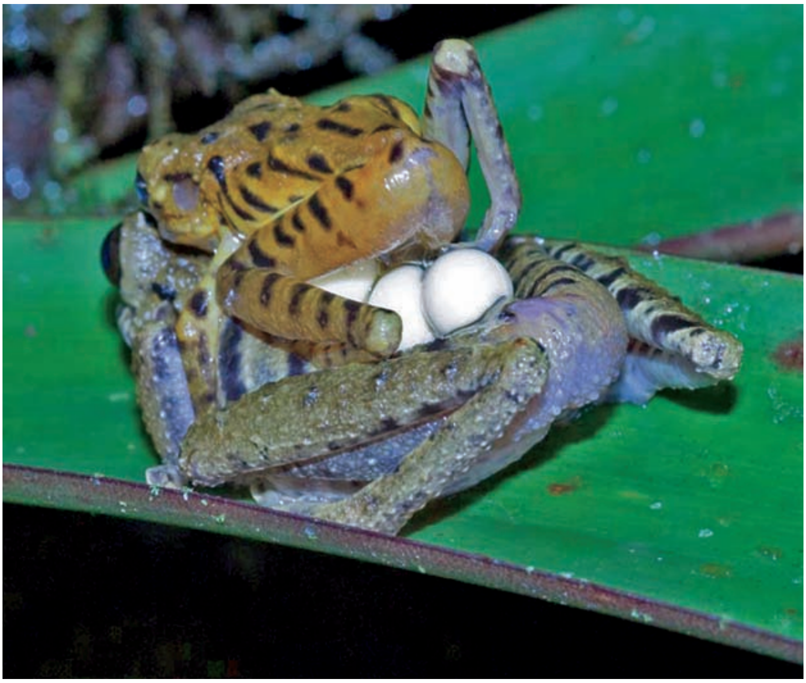

Fig. 7.3 Amplectant male placing eggs with his hind feet during oviposition in *Stefania ayangannae*. Photo by D. B. Means, KUDA.

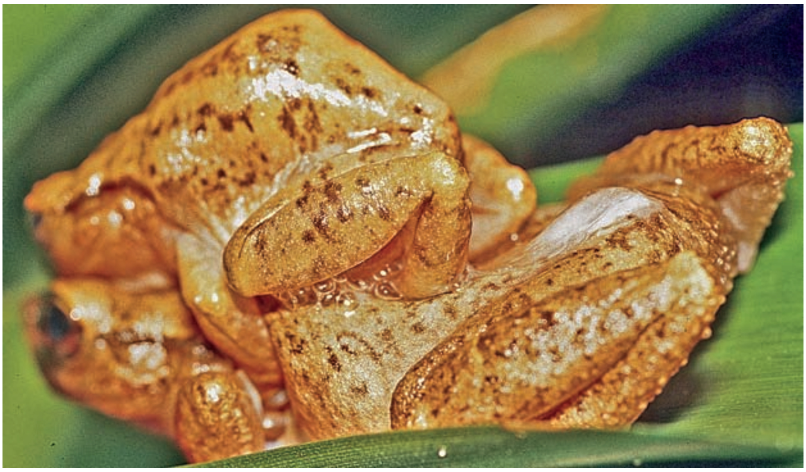

Fig. 7.4 Amplectant pair of *Fritziana goeldii*, showing the elevated posterior part of the female's body. Note mucous being pushed forward by the male's feet. Photo by K.-H. Jungfer, KUDA.

on the dorsum of the female and then use their hind feet to place the eggs on the dorsum or in the pouch of the female (Fig. 7.3). Also, in all observations, the female elevates the posterior part of her body, so the cloaca is in the highest part of the body (Fig. 7.4).

In all hemiphractids in which the eggs develop openly on the dorsum of the female (*Cryptobatrachus*, *Hemiphractus*, and *Stefania*), the eggs presumably are "glued" onto the female. Slight depressions are evident on the female's dorsum while she is carrying eggs or recently hatched young. The female exudes mucous from the cloaca, and this mucous is spread onto the back of the female by pedaling movements of the male's feet (Jungfer and Böhme, 1991). After the young have departed, the female sloughs the mucous (Fig. 7.5). In *Fritziana goeldii*, mucous secreted from the female's cloaca is pushed forward by the male's feet; the male beats the mucous into a foamy mass prior to oviposition, during which the male guides eggs forward on the female's back with his feet (Fig. 7.6).

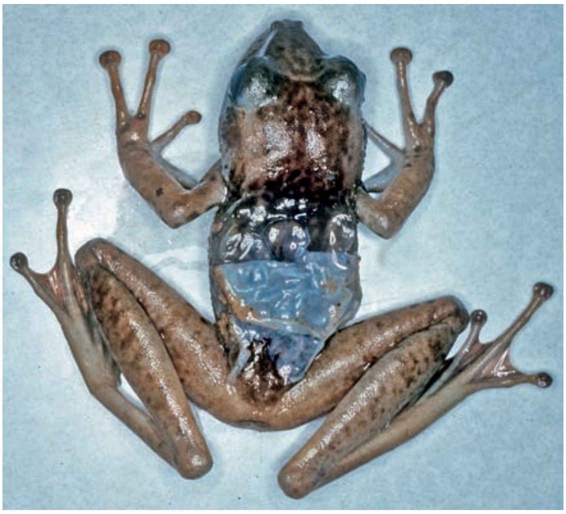

Fig. 7.5 Preserved female of *Stefania scalae*, with the anterior part of the mucoid layer pulled posteriorly, revealing depressions in the dorsal integument. Photo by W. E. Duellman.

Placement of eggs in the pouch by the male has been observed in *Flectonotus pygmaeus* (Duellman and Maness, 1980; Duellman et al., 2011), *Gastrotheca cornuta* (Gagliardo et al., 2010), *G. plumbea* (Auber-Thomay et al., 1990), *G. riobambae* (as *G. marsupiata*) (Hoogmoed, 1967, and references cited therein), and *G. walkeri* (K.-H. Jungfer, pers. comm.). In all of these taxa, the male uses his feet to grasp the eggs as they exit the female's cloaca and then pushes the eggs into the pouch. Mertens (1957) observed similar behavior of an amplectant pair of *G. ovifera*, but he stated that eggs rolled through a secretion (presumably sperm) into the pouch from the female's uplifted cloaca, and that there was little movement of the male's feet. Mertens assumed that eggs moved into the pouch through suction exerted by the dorsal skin of the pouch combined with that of the male's venter, but he may have missed action by the male's feet.

Obviously there are several venues for ovarian development in hemiphractine frogs. Herein, I recognize seven kinds of structures onto which eggs are attached or into which they are inserted (Fig. 7.7). The simplest

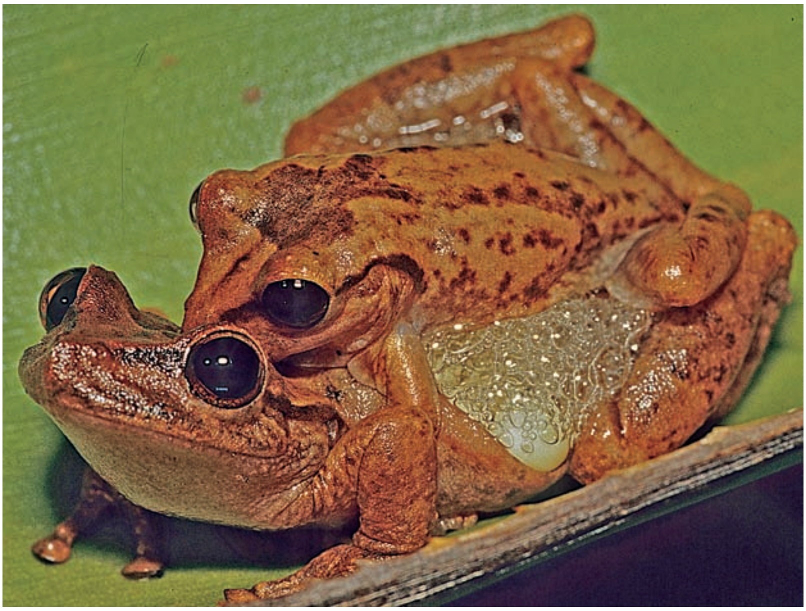

Fig. 7.6 Male *Fritziana goeldii* pedaling mucous into a foamy mass on the back of the female. Photo by K.-H. Jungfer, KUDA.

is the adherence of a small number of eggs onto the back of the female (Fig. 7.7A); this characterizes *Cryptobatrachus*, *Hemiphractus*, and *Stefania*. A basin-like structure (Fig. 7.7B), defined by lateral folds of varying heights, is found in *Fritziana*. In *Fr. fissilis*, the folds even touch middorsally, but margins of the folds do not fuse to form an enclosed pouch, as in *Flectonotus* (Fig. 7.7C). In all *Gastrotheca*, the eggs develop in a closed pouch on the back of the female; large eggs that undergo direct development usually are arranged in a single layer (Fig. 7.7D), whereas small eggs that hatch as tadpoles are stacked in multiple layers within the pouch (Fig. 7.7E). In two species of *Gastrotheca* (*G. antoniiochoai* and *G. zeugocystis*), the pouches are expanded laterally, so the eggs undergo direct development on the sides of the body of the female (Fig. 7.7F). In two other species of *Gastrotheca* (*G. walkeri* and *G. williamsoni*), the pouch is expanded laterally and extends through a slit in the body wall; thus the eggs undergo direct development within the coelomic cavity (Fig. 7.7G). These pouches are termed retroperitoneal.

On initial inspection, Figure 7.7 suggests an evolutionary trend from the simplest site of egg development (openly on the dorsum of the female) to the most advanced (retroperitoneal pouches), but the phylogenetic tree of hemiphractids shows that this is not so. The open pouch of *Flectonotus*, the basin-like structure of *Fritziana*, and the closed pouch of *Gastrotheca* all were derived independently (Fig. 7.8). Likewise, mul-

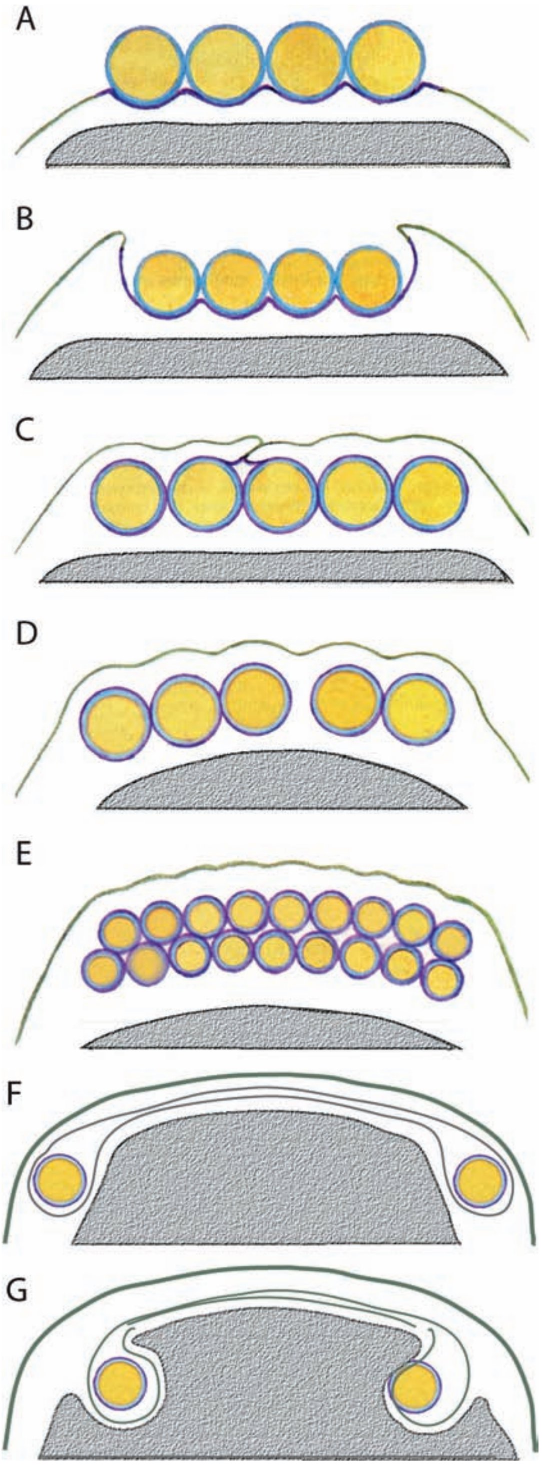

Fig. 7.7 Diagrammatic cross-sections of bodies of females, showing the pouch structure and position of the eggs. A: *Cryptobatrachus*, *Hemiphractus*, and *Stefania*. B: *Fritziana*. C: *Flectonotus*. D: direct-developing *Gastrotheca*. E: tadpole-producing *Gastrotheca*. F: *G. antoniiochoai* and *G. zeugocystis*. G: *G. walkeri* and *G. williamsoni*.

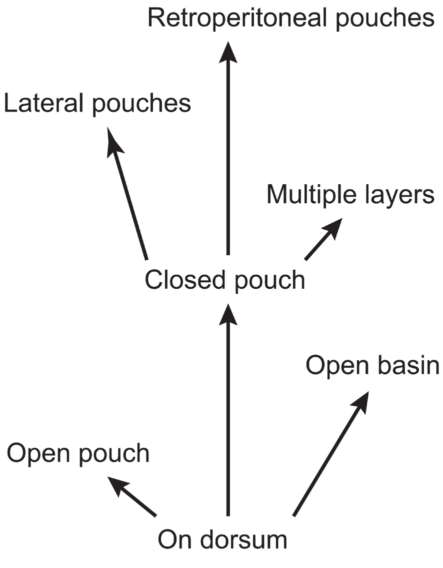

Fig. 7.8 Evolutionary trends in the site of egg development in hemiphractid frogs.

tiple layers of eggs in a pouch, lateral pouches, and retroperitoneal pouches were derived independently from a simple dorsal pouch.

The Brood Pouch

In his thorough description and discussion of the brood pouch in *Gastrotheca ovifera*, Weinland (1854) considered the pouch to be formed by a dermal invagination. In contrast, Brandes and Schoenichen (1901) studied pouch formation in *Flectonotus pygmaeus* and concluded that the pouch was formed by two longitudinal lateral folds of skin that grew together middorsally but left a small opening posteriorly. They were correct with respect to *Fl. pygmaeus* and assumed that the pouch in *Gastrotheca* was formed in the same manner. Gadow (1901) agreed with Weinland (1854) about the formation of the pouch in *Gastrotheca* and noted that the lateral folds of skin in *Fritziana goeldii* might be an incipient brood pouch. Gadow (1901) interpreted the brood pouch of *Fl. pygmaeus* to have developed in the manner independently described by Brandes and Schoenichen (1901), but, he stated (1901:203), "the suggestion that this seam is burst open, in order to set the full-grown young free, instead of their passing through the existing opening, is scarcely credible." Andersson (1911) supported Weinland's (1854) contention that the brood pouch was formed by dermal invagination and disagreed with Brandes and Schoenichen's (1901) opinion that the pouch in *Gastrotheca* originated in the same manner as in *Flectonotus*.

Jones et al. (1973) experimentally induced estrogen into subadult female *Gastrotheca riobambae*. After 24 days, a pair of longitudinal ridges developed posterior to the sacrum; their subsequent adhesion formed a pouch. During this development, there was either a decrease or a loss of epidermal keratin, dermal chromatophore units, and serous glands. As they noted, the skin in the pouch has many mucous glands and exhibits dermal hypervascularity and connective tissue hyperplasia. Del Pino et al. (1975) thoroughly described the pouch structure in *G. riobambae*. Epidermal tissues with capillaries extend from the lining of the pouch between the eggs, thereby forming partial chambers for each egg. After the birth of young or the release of tadpoles, the pouch vascularization is resorbed; furthermore, the outer layers of epithelial cells are shed and there is tissue reorganization. Thus it seems that pouch formation in *G. riobambae*, an advanced hemiphractid, occurs in the same way as in the basal *Flectonotus*. Intensive studies on the development of *G. riobambae* by del Pino (1980) confirmed the results by Jones et al. (1973).

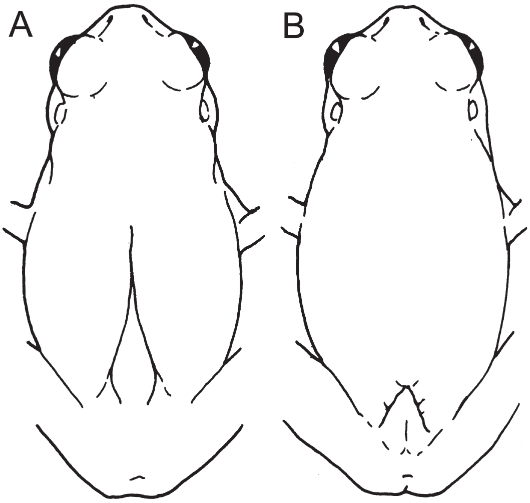

Fig. 7.9 Diagrammatic representation of apertures to the brood pouches in female *Gastrotheca*. A: typical of the subgenera *Cryptotheca*, *Eotheca*, and *Opisthodelphys*. B: typical of the subgenera *Duellmania* and *Gastrotheca*.

In del Pino's (1980) comparison of pouch structures in several species of *Gastrotheca*, she recognized six types of pouches. Most importantly, her pouch-type two is characteristic of all brooding females in the basal *Gastrotheca* (subgenera *Cryptotheca*, *Eotheca*, and *Opisthodelphys*) that have been examined. In these frogs, the pouch is restricted to the posterior portion of the back and is divided into left and right halves by a membranous extension of the V-shaped aperture. In some species, the arms of the V extend posteriorly and may help guide the eggs into the pouch (Fig. 7.9A). In the other subgenera (*Australotheca*, *Duellmania*, and *Gastrotheca*) the pouch extends over the entire back and sometimes onto the flanks; the pouch opening is puckered from a U-shaped or shallow V-shaped aperture (Fig. 7.9B). Thus pouch structure has some phylogenetic significance (Fig. 7.1).

Embryonic Development

The discovery of multinucleated oogenesis in hemiphractid frogs by del Pino and Humphries (1978) revealed a previously unknown early embryonic phenomenon. They showed that a lack of cytoplasmic divisions following nuclear divisions resulted in oocytes having more than 2000 nuclei in *Flectonotus pygmaeus*. Subsequently, as oogenesis proceeds, the number of nuclei is reduced to one. The original descriptive study on hemiphractid oogenesis was followed by more quantitative and molecular studies in Macgregor and del Pino (1982). Elinson et al. (1990) reported the number of nuclei for 35 species of hemiphractine frogs. Multinucleate oogenesis was found in *Flectonotus*, *Stefania*, and in the subfamilies *Australotheca*, *Cryptotheca*, *Eotheca*, and *Opisthodelphys* of *Gastrotheca*. With the exception of *G. griswoldi*, all other *Cryptobatrachus*, *Fritziana*, *Gastrotheca*, and *Hemiphractus* examined had mononucleate oogenesis.

The early development of *Gastrotheca riobambae* has been thoroughly examined by del Pino, who synthesized her work in Schmid et al. (2012). The most recent comparative study of eight species in five families (del Pino et al., 2007) included *G. riobambae*, which was analyzed mostly in connection with *Xenopus laevis*. Nonetheless, these comparisons provide no insights for interpreting embryonic development in hemiphractid frogs. Investigations into the early development of *G. riobambae* revealed the presence of a disc around the blastopore (del Pino and Elinson, 1983; Elinson and del Pino, 1985). To date, this embryonic disc has not been observed in the few other frogs examined, none of which was a hemiphractid (del Pino et al., 2007; Moya et al., 2007). Another possible feature of hemiphractids is the amount of time until blastopore formation: 14 hours in *X. laevis*, 4 days in *Epipedobates* [= *Colostethus*] *machalilla*, and 14 days in *G. riobambae* (del Pino, 1996; del Pino et al., 2004). Again, the use of such developmental features in an evolutionary context is not possible until many more taxa are studied.

In a seminal paper on frog reproduction, Salthe and Duellman (1973) compared various size factors (female snout–vent length, diameter of eggs, and clutch size) in different reproductive modes. They reported that in species with direct development, eggs tend to be larger and clutches smaller than those that hatch as aquatic larvae. Their results are evident in the comparisons made among species of *Gastrotheca* (Fig. 7.10).

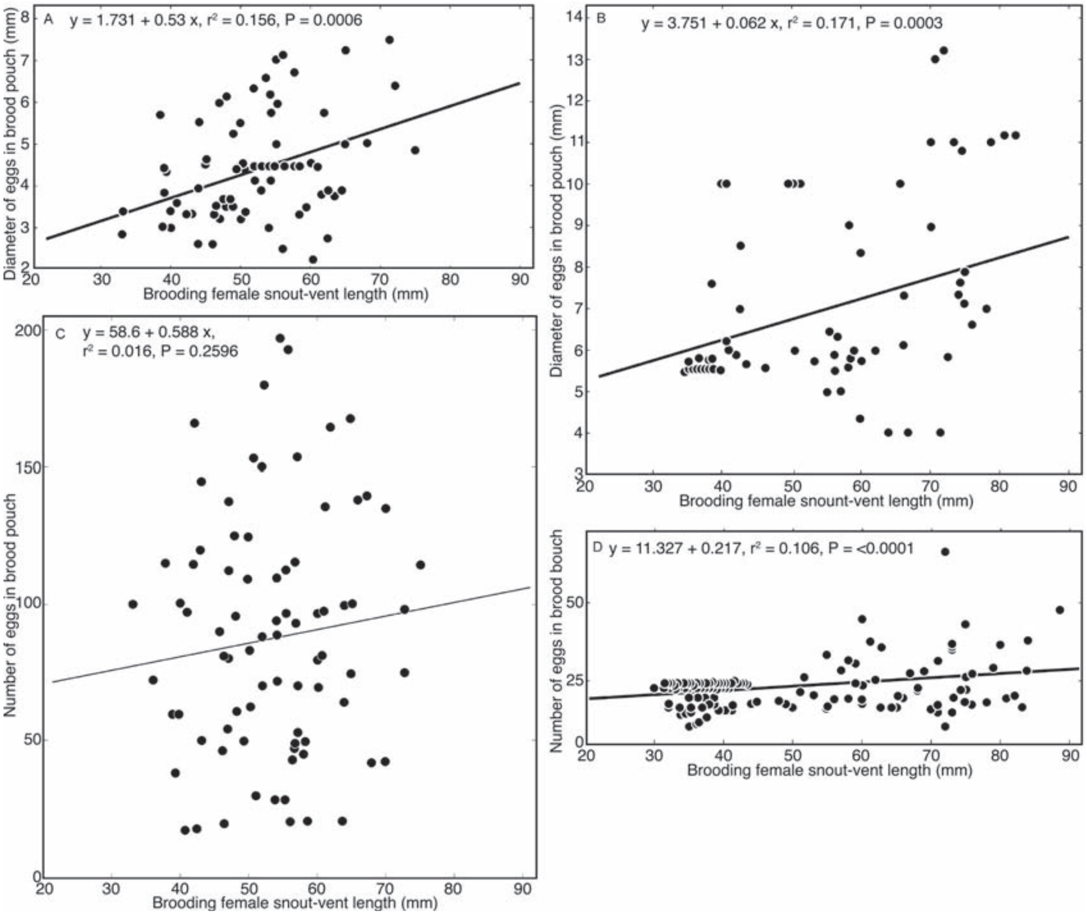

Fig. 7.10 Straight-line regression analyses, showing relationships between the female's snout–vent length and the diameter and number of eggs in the brood pouches of *Gastrotheca* producing eggs that hatch as tadpoles (A and C) and those that undergo direct development (B and D). Dots represent individuals.

These graphs clearly show that frogs with eggs that undergo direct development brood fewer and larger eggs than those species in which the eggs hatch as tadpoles. Furthermore, the graphs show that in tadpole-producing species, larger frogs brood larger clutches than smaller species, whereas there is no equally clear relationship in direct-developing species.

Females in genera other than *Gastrotheca* have large eggs that hatch as non-feeding tadpoles or as froglets. In the small taxa that have eggs hatching as non-feeding tadpoles, the number of embryos brooded, their volume, and the total volume of the clutch are correlated significantly with snout–vent length (Duellman and Gray, 1983); mean clutch size varies from 3.3 in the small *Flectonotus fitzgeraldi* to 15.4 mm in *Fritziana goeldii*. Further studies of *Fr. goeldii* by Weygoldt and Carvalho-e-Silva (1991) and Duellman et al. (2011) showed that this species brooded 9–22 eggs ($\bar{x} = 14.8$, $n = 27$).

In eight species of *Stefania* for which brooding females are known, there is a strong correlation of the number of eggs with the snout–vent length of the brooding female (Salerno and Pauley, 2012). Mean clutch size in *Stefania* ranges from 5.4 in the smallest species (*S. satelles*, with a mean snout–vent length of 53.2 mm) to 18.6 in the largest species (*S. evansi*, with

Table 7.1 Female body size and ovarian factors in *Gastrotheca*. Measurements are in mm; means, in parentheses. The number of eggs in taxa denoted by an asterisk (*) are for ovarian eggs; others are for eggs in brood pouches.

Species	*n*	Female SVL	Number of eggs	Diameter of eggs	Stage at hatching
G. abdita	8	39.0–46.2 (42.5)	12–21 (14.6)	5.8–7.6 (6.8)	46
G. albolineata	1	60.0	16	—	46
G. andaquiensis	1	76.0	14	—	46
G. argenteovirens	8	54.6–67.9 (58.0)	20–55 (37.5)	4.2–5.3 (4.8)	37
G. aureomaculata	3	72.6–75.0 (73.6)	76–116 (97.6)	5.1–7.5 (6.4)	32
G. christiani	11	35.5–39.3 (37.2)	10–17 (13.1)	5.4–5.8 (5.6)	46
G. cornuta	4	70.5–76.4 (72.8)	5–12 (9.2)	9.2–13.0 (11.0)	46
G. dendronastes	1	69.3	11	9.0	46
G. dunni	3	42.9–50.5 (46.3)	32–46 (43.0)	4.6–6.0 (5.3)	37
G. excubitor	2	37.6–42.0 (39.3)	17–22 (19.5)	6.0	46
*G. excubitor**	32	29.7–41.8 (36.3)	24–22 (20.5)	—	46
G. fissipes	1	81.5	16	10.0	46
G. galeata	4	48.5–51.1 (49.7)	12–24 (17)	10.0	46
G. gracilis	3	39.2–50.0 (44.0)	60–68 (60.4)	4.5	32
G. griswoldi	6	36.1–40.5 (38.8)	20–22 (21.3)	—	46
G. guentheri	3	71.0–82.0 (75.1)	12–15 (13.0)	11.0–13.2 (11.8)	46
G. helenae	2	62.5–64.9 (63.7)	12	—	46
G. lateonota	11	54.6–63.7 (58.9)	64–152 (103.2)	5.3–7.2 (6.1)	32
G. litonedis	3	49.0–56.7 (52.4)	53–75 (72.0)	5.3–6.3 (5.8)	31
G. longipes	1	82.5	17	11.2	46
G. marsupiata	14	33.7–49.4 (40.5)	20–113 (77.6)	1.7–4.3 (3.7)	31
G. microdiscus	3	62.5–75.0 (67.2)	12–24 (19.7)	8.0–10.0 (9.0)	46
G. monticola	8	57.4–66.3 (61.3)	72–169 (104.5)	2.3–4.9 (3.9)	32
G. nicefori	3	60.3–75.2 (69.8)	26–37 (32.0)	7.2–11.0 (8.8)	46
*G. ochoai**	13	31.7–36.2 (34.2)	10–22 (19.6)	—	46
G. orophylax	14	50.8–74.0 (59.3)	12–37 (23.4)	5.2–7.5 (6.2)	46
G. ovifera	9	73.8–88.0 (79.9)	20–48 (32.0)	6.6–11.0 (8.5)	46
*G. pacchamama**	4	35.1–37.0 (36.7)	5–8 (6.2)	—	46
G. plumbea	5	60.3–71.0 (66.0)	24–34 (26.4)	4.0–5.9 (4.5)	46
G. pseustes	13	47.4–59.5 (53.5)	53–197 (110.2)	2.6–6.1 (4.0)	31
*G. rebeccae**	1	44.2	22	—	46
G. riobambae	12	44.3–62.2 (50.9)	66–166 (122.4)	2.7–5.6 (4.2)	31
G. ruizi	1	50.1	124	4.4	31
G. stictopleura	1	62.3	82	5.3	32?
G. testudinea	3	59.4–72.5 (63.8)	30–69 (47.7)	5.5–9.1 (6.7)	46
G. trachyceps	3	63.8–69.8 (66.8)	22–47 (34.1)	5.3	37
G. walkeri	4	55.0–66.8 (61.8)	13–21 (16.2)	—	46
G. weinlandii	1	78.8	14	7.0	46

a mean snout–vent length of 76.9 mm). The largest clutch size reported by Salerno and Pauley is 30 eggs, in *S. evansi*. Lynch (2008) reported clutches of 6–39 eggs being brooded by *Cryptobatrachus*; Duellman (1970) observed clutches of 12–14 eggs in *Hemiphractus panamensus* [= *H. fasciatus*], and Salthe and Duellman (1973) noted 10 eggs being brooded by *H. scutatus*.

In direct-developing species of *Gastrotheca*, clutch size is small and eggs are relatively large, in comparison with the large clutch size with relatively small eggs in those species producing feeding tadpoles (Table 7.1). By determining the mean volume of eggs in a clutch and multiplying this volume by the number of eggs in a clutch, it is possible to determine the approximate volume of the clutch. A comparison of clutch volume with size of the brooding female shows that there is no significant difference among the different reproductive modes (Fig. 7.11). Thus marsupial frogs of approximately the same size have egg clutches of proportionally the same volume (= caloric value). Hemiphractid embryos, as well as pipids and presumably all terrestrial breeding frogs, receive no nutrients from the mother; del Pino et al. (1975) and Weygoldt (1976) demonstrated that *G. riobambae* and *Pipa carvalhoi*, respectively, maintain the same dry weights of eggs throughout development. Therefore, the amount of yolk determines both the amount of energy provided to the developing embryo and the stage at which the embryo will hatch. The production of froglets requires eggs with more yolk than does the production of tadpoles. Thus completely endogenous development results in fewer offspring than exogenous development, in which tadpoles feed to obtain much of the energy required for further growth.

For decades it was assumed that the ancestors of frogs with non-feeding tadpoles were lineages with free-living feeding tadpoles, and that the former gave rise to frogs with direct development. As was first suggested by Wassersug and Duellman (1984), this is not the case. In the embryonic development of frogs in families other than Hemiphractidae, there are few or no larval features; both forelimbs and hind limbs develop early and a tail, if present, is short, as in *Eleutherodactylus coqui* (Townsend and Stewart, 1985). In direct-developing hemiphractids, the embryos are tadpole-like (Fig. 7.12). Wassersug and Duellman (1984) examined the external and oral anatomy of tadpoles and embryos of 22 species of hemiphractids. Surprisingly, they found varying amounts of oral structures of tadpoles in the embryos of some direct-developing hemiphractids.

Small filamentous gills develop in early embryos of eleutherodactylid, ceratobatrachid, and microhylid frogs that undergo direct development; later in their development, these gills are resorbed. No such gills occur in embryos of hemiphractids, except in those species of *Gastrotheca* that have free-living tadpoles and in some *Gastrotheca* species that have direct development. Embryos of direct-developing *Gastrotheca* pass through the same early stages as those of post-hatching tadpoles. Within *Gastrotheca*, the degree of development of five kinds of buccal structures was compared among tadpole-producing species with those having direct development. The categories were (1) keratinized mouthparts, (2) gill filters, (3) ventral velum and branchial food traps, (4) filamentous gills, and (5) buccal projections and papillations. All of these structures are fully developed in tadpoles of *Gastrotheca*. Among direct-developing *Gastrotheca*, the greatest development of larval buccal structures is in *G. orophylax*, fol-

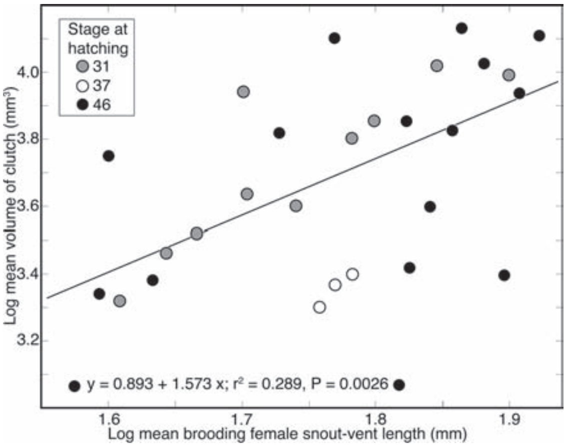

Fig. 7.11 Straight-line regression analysis, showing the relationship of the volume of egg clutches and female body size of *Gastrotheca*, with respect to the stage at hatching. The symbols are means of species.

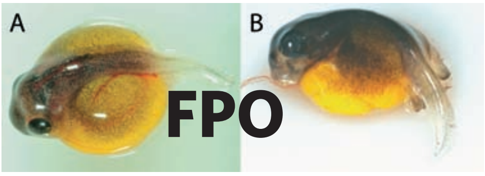

Fig. 7.12 Embryos of *Gastrotheca excubitor* from a female obtained at Llamawasi, near Acjanaco, 3500 m, Cusco, Peru. The external gills are removed; the diameter of the yolk is about 4 mm. *Left*: The tadpole-like appearance of an early developmental stage. *Right*: Hind limb buds. Of all direct-developing frogs, only the embryos of hemiphractid frogs pass through tadpole stages in their embryonic development. Photos by A. Catenazzi, KUDA.

lowed by *G. chrysosticta* and *G. nebulanastes* (reported as *G. excubitor* by Wassersug and Duellman, 1984). Structures are greatly reduced in the other species examined. Keratinized mouthparts are absent in embryos of *G. cornuta*, *ovifera*, *testudinea*, and *walkeri*; *G. cornuta* and *G. walkeri* have only vestiges of the larval buccal structures.

None of the larval buccal structures is present in embryos of *Cryptobatrachus* and *Hemiphractus*; two structures are vestigial in *Stefania*, and all are reduced or absent in *Flectonotus* and *Fritziana*. The buccal structures of direct-developing hemiphractids are identical to those features at some point in the early development of free-living *Gastrotheca* tadpoles. Embryonic development may proceed to hatching as a froglet if sufficient yolk is available and genetic regulation shuts down the complete development of tadpole features. Auber-Thomay et al. (1990) reported brooding *G. plumbea* basking in sunlight. This behavior suggests that possibly UVB radiation or heat enhances development.

Little information exists on the duration of development. Del Pino and Escobar (1981) stated that *Gastrotheca riobambae* raised in the laboratory in Quito, Ecuador, required about 103 days from their birth as tadpoles until metamorphosis. This is much longer than a development period of 41 days for tadpoles of the same species in Leiden, Netherlands (Hoogmoed, 1967). Duration of development has not been reported for any other species of *Gastrotheca* having feeding tadpoles, but duration of development has been noted for three direct-developing species of *Gastrotheca*: 60 days from oviposition to birth in *G. christiani* (Barrio, 1976), 60–80 days in *G. cornuta* (Gagliardo et al., 2010), and 4 months in *G. testudinea* (L. Coloma, pers. comm.). The duration of development is even less in taxa having non-feeding tadpoles: 34–43 days in *Flectonotus pygmaeus* and 38–42 days in *Fritziana goeldii* (Duellman et al., 2011). The great disparity between *G. riobambae* and the other species has yet to be understood, but temperature probably is an important factor.

Comparatively rapid development occurs in unrelated frogs having direct development of terrestrial eggs. Hatching occurs at 17–36 days after oviposition in the Puerto Rican *Eleutherodactylus coqui* (Townsend and Stewart, 1985) and 29–30 days in the Fijian ceratobatrachid *Platymantis vitiana* (Narayan et al., 2011).

Embryonic Respiration

The gaseous exchange of oxygen and nitrogenous wastes in aquatic eggs is accomplished by diffusion across the membranous egg capsule; differential osmotic pressure necessitates nothing more than small highly vascularized gills to accomplish a sufficient exchange in these embryos. Osmotic pressures differ in terrestrial eggs, which require vascularized embryonic tissues to maintain an adequate exchange with their non-aquatic environment. Such tissues are in the form of thin highly vascularized fan-like tails in terraranans, as demonstrated for *Eleutherodactylus* by Townsend and Stewart (1985) and asterophryine microhylids by Bickford (2004). The same is characteristic of the rhacophorid genus *Philautus* (Bahir et al., 2005). Ceratobatrachid frogs have highly vascularized lateral abdominal sacs (Narayan et al., 2011). In all of these taxa, the highly vascularized embryonic structures are in close contact with the vitelline membrane of the egg, thereby permitting a gaseous exchange with the environment.

Marsupial frogs and their relatives in Hemiphractidae have a unique embryonic respiratory system. Early in their embryonic development, gill buds appear from the first branchial arch in *Cryptobatrachus* and *Flectonotus*, and from the first and second branchial arches in the other genera. These eventually become gill stalks with afferent and efferent blood vessels; the ends of the stalks spread out to form a highly vascularized gill (Fig. 7.13). There seems to be an evolutionary progression in gill development.

Although data exist for only a few species, it seems that embryos of species of *Cryptobatrachus* and *Flectonotus* have a single pair of gills, each with a gill stalk derived from Branchial Arch I. The gills are small and only cover the head and anterior part of the body (Fig. 7.14A). Other genera of hemiphractids have two pairs of gills. These are small and cover only part of the body in *Fritziana*, whereas in *Hemiphractus* and *Stefania* there two pairs of large gills; each gill has a gill stalk derived either from Branchial Arch I or II (Fig. 7.14B). In *Gastrotheca*, the gills on either side of the body are fused into a large bell-shaped gill with two gill stalks (Fig. 7.14C). In three subgenera of *Gastrotheca* (*Australotheca*, *Duellmania*, and *Gastrotheca*) the gill stalks on each side of the body are fused, so there is only a single stalk (Fig. 7.14D). Thus within Hemiphractidae there is an evolutionary progression from a single pair of small gills to two pairs of large gills that subsequently become fused.

The gills of *Flectonotus* and *Gastrotheca* undergo a gaseous exchange with maternal tissues in the pouch. In *Cryptobatrachus*, *Hemiphractus*, and *Stefania*, the eggs are adherent to a mucoid layer on the back of the brooding female. For these genera, it is unlikely

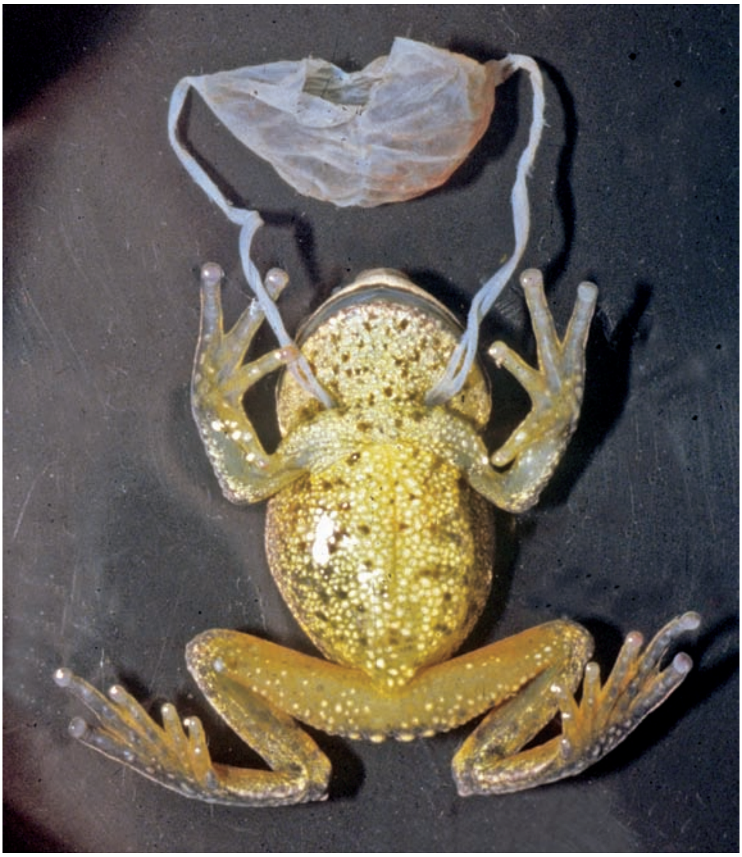

Fig. 7.13 Hatchling from a female *Gastrotheca helenae* (ICN 10552). Note the two pairs of gill stalks entwined and attached to single fused gill. Photo by P. M. Ruíz-C., KUDA.

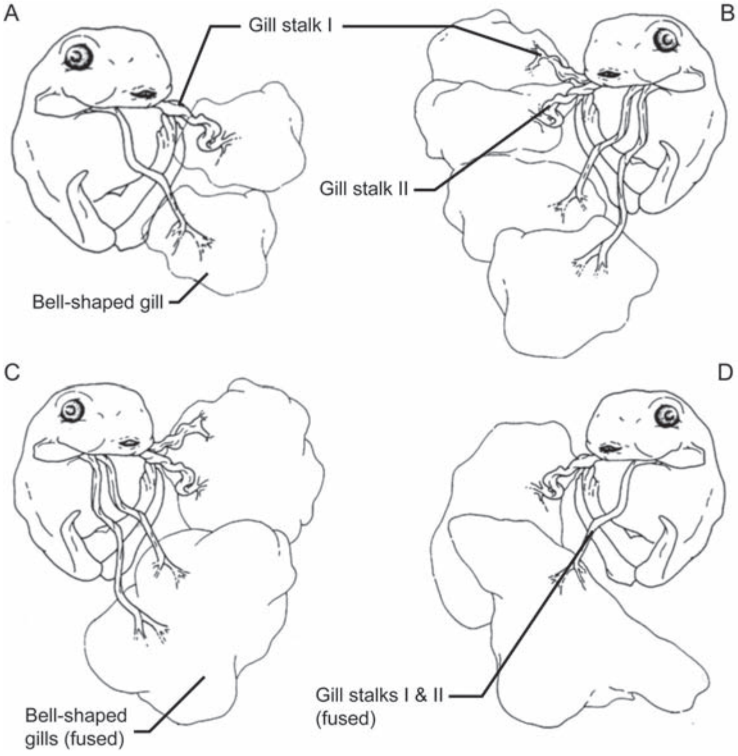
A
Gill stalk I
B
Gill stalk II
Bell-shaped gill
C
D
Bell-shaped
gills (fused)
Gill stalks I & II
(fused)

Fig. 7.14 Diagrammatic representations of embryos of hemiphractid frogs, showing the relative sizes of the external gills and the number and condition of the gill stalks. A: *Cryptobatrachus* and *Flectonotus*. B: *Fritziana*, *Hemiphractus*, and *Stefania*. C: basal *Gastrotheca*. D: advanced *Gastrotheca*. Adapted from Mendelson et al. (2000).

that any gaseous exchange takes place with maternal tissues; instead, a gaseous exchange occurs with the environment. The embryos in the pouches of *Flectonotus* and on the backs of *Cryptobatrachus* have a single pair of small gills, whereas two pairs of large gills exist in the other taxa, whether in pouches (*Gastrotheca*) or openly on the backs of females *(Hemiphractus* and *Stefania*). Thus the number and sizes of gills are not correlated with the place of embryonic development.

Hatching

Again, data are available for only a few species of hemiphractids. Nonetheless, there seem to be family-wide characteristics. For example, hatching is accomplished without the aid of the egg tooth that is characteristic of *Eleutherodactylus* and its relatives. Another possible family-wide feature may be the simultaneous hatching of eggs that has been observed in some species of *Gastrotheca* and reported in *Cryptobatrachus fuhrmanni* by Lynch (2008). This suggests a possible hormonal release in those taxa having a pouch, but what about those with the mucoid layer separating the embryos from maternal tissues? For genera in which eggs adhere to a mucoid layer on the backs of brooding females (*Cryptobatrachus*, *Hemiphractus*, and *Stefania*), one or more gills may remain attached to the mucoid layer after hatching (Fig. 7.15), thereby permitting the young frogs to ride on the mother's back.

When the tadpoles hatch in the pouch of *Gastrotheca*, the larvae are extremely active. The female enters water and uses her third and fourth toes to stretch the pouch opening, whereupon tadpoles move from the pouch into the water (Fig. 7.16). Usually the tadpoles have sloughed off their external gills by the time they leave the pouch. The female uses her feet to scoop out the last of the tadpoles and shed gills and disintegrating tissue from inside the pouch. This type of parturition has been observed in *G. lojana*, *marsupiata*, and *riobambae*. Among the large species with V-shaped apertures of their pouches (e.g., *G. cornuta* and *G. ovifera*), hatchlings simply walk out of the pouch, but the female may hasten their exodus by removing hatchlings with her feet. For these species, usually the gills are sloughed off

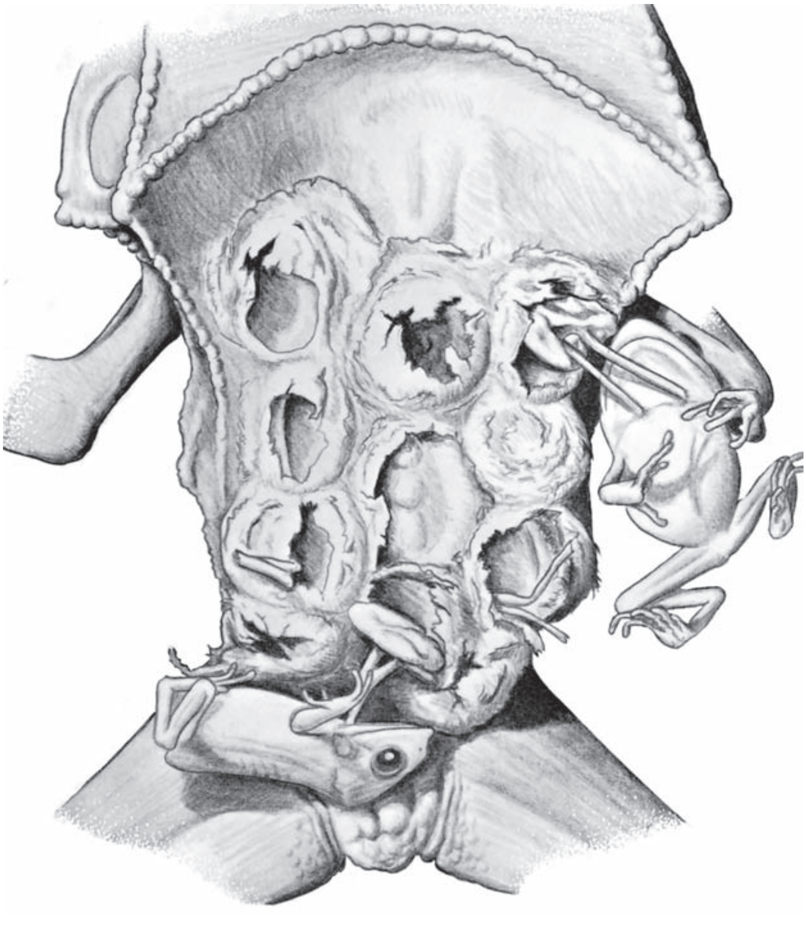

Fig. 7.15 Dorsum of a preserved postpartum female *Hemiphractus fasciatus* (BYU 19142) from Río Changena, Bocas del Toro, Panama. Note the remnants of a hardened mucous covering, depressions in the dorsal skin, and the attachment of the hatchlings' gills. Duellman (1970).

before emergence. The birth of young in the smaller *G. nebulanastes*, with a U-shaped pouch opening, is somewhat different. Each newborn is enclosed by gills upon its emergence from the pouch; essentially the entire froglet is out of the pouch before the gills are sloughed, sometimes aided by the froglet kicking its feet (Fig. 7.17). During the final stages of parturition, part of the pouch lining is protruded as the female inserts one or both feet in the pouch to remove the young, undeveloped eggs, and detritus. This manner of parturition also has been observed in *G. christiani*, *orophylax*, and *plumbea*.

Tadpoles exit the pouch in *Gastrotheca riobambae*

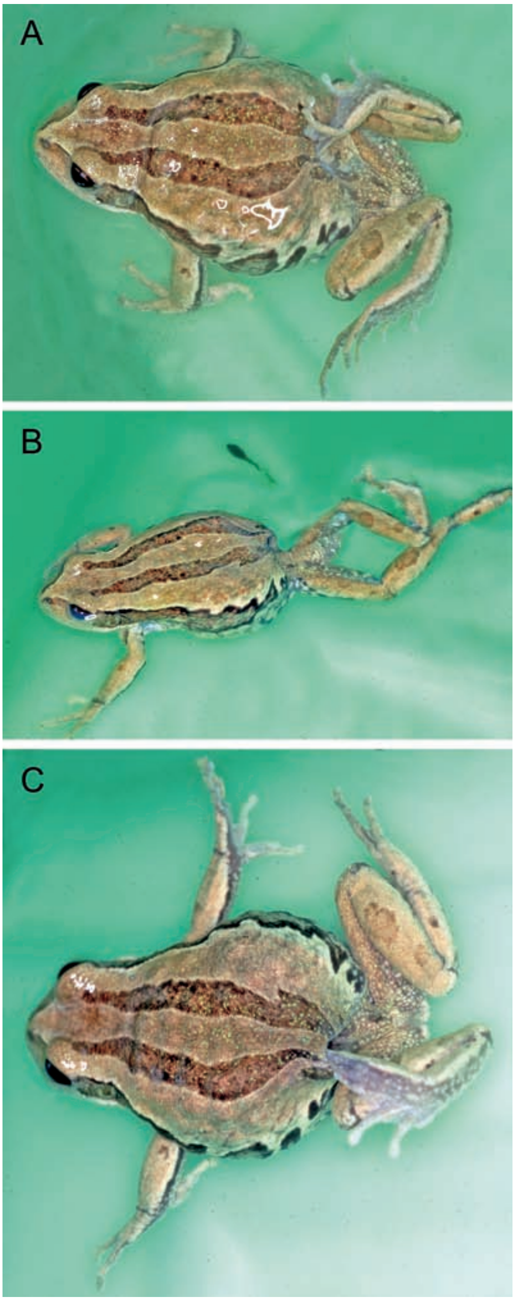

Fig. 7.16 Parturition of tadpoles by a captive female *Gastrotheca riobambae* from Guano, Chimborazo, Ecuador. A: female opening the pouch. B: tadpoles leaving the pouch. C: female using a hind foot to pull tadpoles from the pouch. Photos by W. E. Duellman.

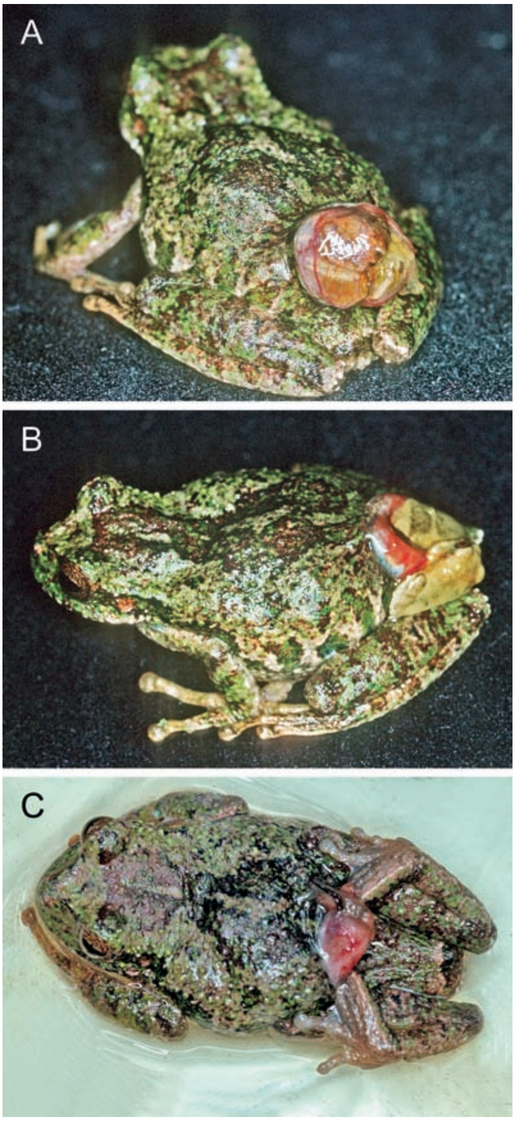

Fig. 7.17 Parturition of direct-developing young by *Gastrotheca nebulanastes* (KU 173208), from Buenos Aires, Cusco, Peru. A: first hatchling, with a gill encompassing the body. B: second and third hatchlings, devoid of gills. C: female pulling a hatchling from the pouch by using her hind feet. Photos by W. E. Duellman.

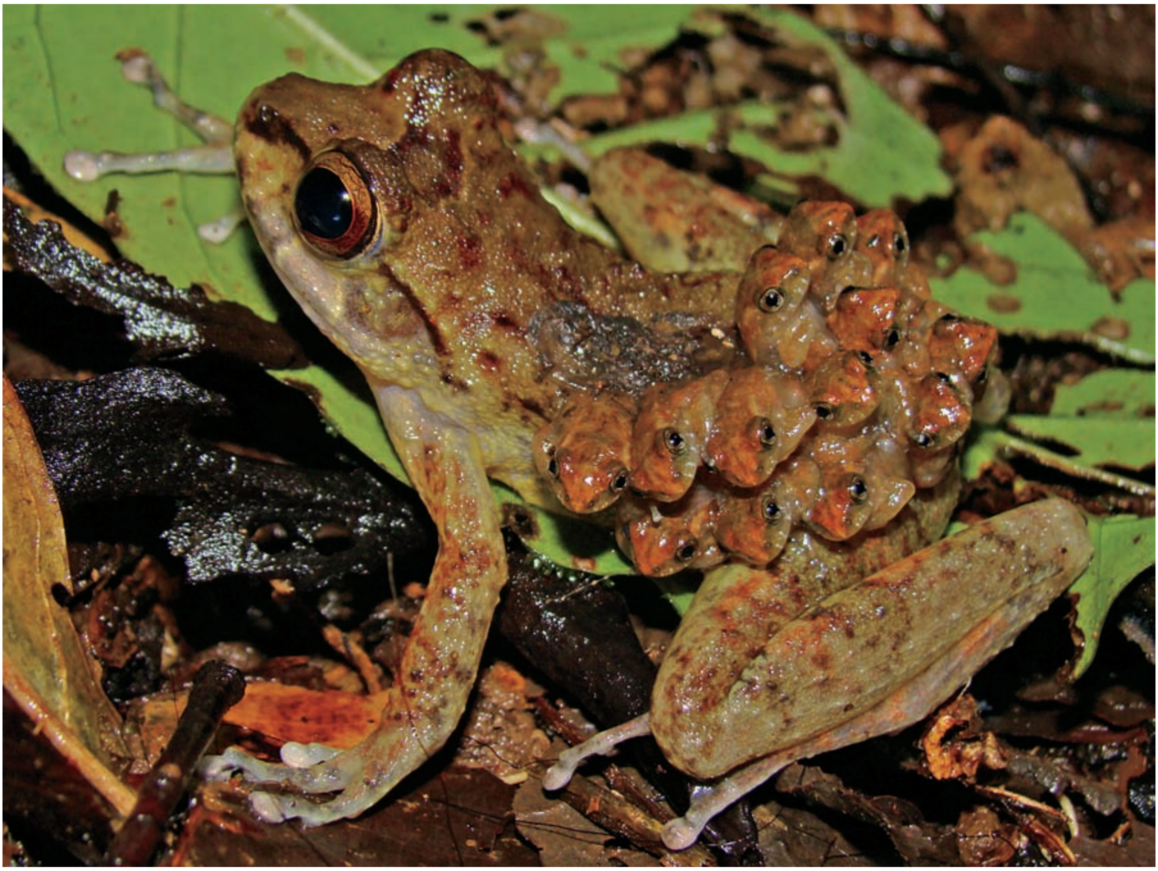

Fig. 7.18 Simultaneous emergence of hatchling *Cryptobatrachus remotus* from Península de Perijá, Trujillo, Venezuela. Photo by F. J. M. Rojas-Runjaic, KUDA.

within only a few minutes. Parturition in *G. ovifera* required about 5 hours, whereas the birth of 16 young by a *G. nebulanastes* female required nearly 10 hours. At least within two species of *Cryptobatrachus*, there is a simultaneous hatching of eggs into froglets; Lynch (2008) noted this in *C. fuhrmanni*, and Figure 17.18 shows this clearly in *C. remotus*.

Larvae

Two entirely different kinds of tadpoles are known in Hemiphractidae: the non-feeding tadpoles of *Flectonotus* and *Fritziana*, and feeding tadpoles of *Gastrotheca*. The tadpoles of *Flectonotus* are obligatory non-feeders. At the time of hatching, the brooding female moves to water found in a bromeliad. Newly hatched tadpoles (Stage 41) have well-developed hind limbs. The spiracle is sinistral, short, attached to the body wall, and ventrolateral in position; its opening is directed posteriorly, at about midlength of the body. The oral disc lacks marginal papillae; labial teeth are absent, and the beaks are weakly cornified, if at all (Figs. 7.19A and C). The forelimbs appear after 5–7 days in the non-feeding tadpoles of *Fl. pygmaeus*, which metamorphose after 11–15 days (Duellman and Maness, 1980). Yolk in the intestines provides all of the nourishment needed for larval life. The eggs of *Fritziana* hatch earlier, at Stages 30–33 (Weygoldt and Carvalho-e-Silva, 1991); these tadpoles are facultative non-feeders and develop in water-filled cavities in bromeliads or, for *Fr. fissilis*, in bamboo. The spiracle is short, adherent to the body wall just left of the midline, and directed posteriorly at about midlength of the body. The oral disc of the tadpole has blunt marginal papillae; the larval beak is keratinized, but labial teeth are absent (Figs. 7.19B and D). Some recently hatched tadpoles of *Fr. goeldii* ate the remains of the egg sac and any unfertilized eggs or dead embryos that were in their clutch. These tadpoles, and those that did not feed, metamorphosed in 10–15 days after hatching, again showing that the nourish-

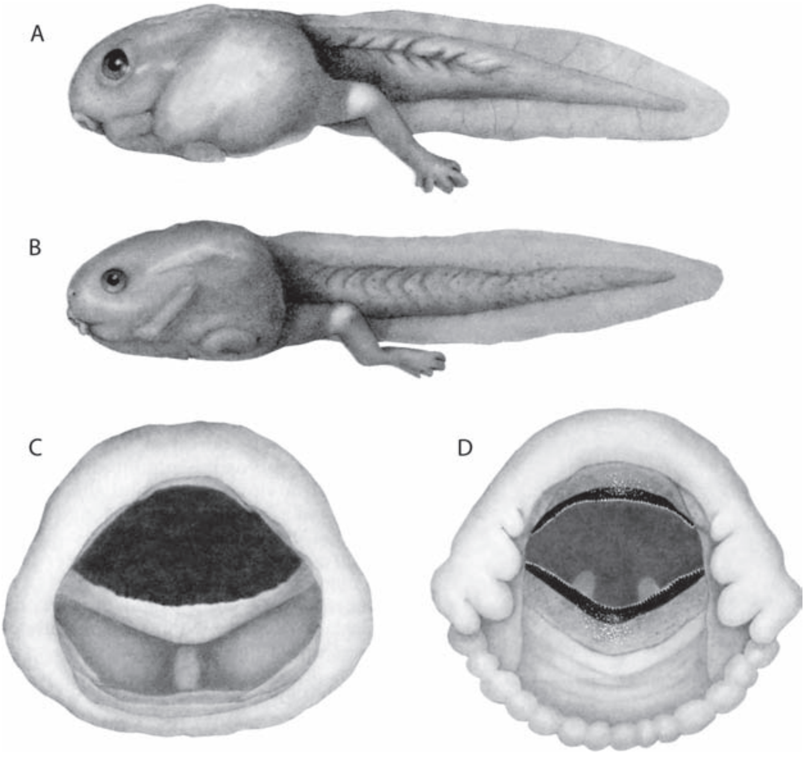

Fig. 7.19 Lateral views (A and B) of hatchling non-feeding tadpoles and anteroventral views (C and D) of oral discs. A and C: *Flectonotus fitzgeraldi* (AMNH 87397), from Tamana Caves, Trinidad. B and D: *Fritziana fissilis* (MNRJ 1998), from Angra dos Reia, Rio de Janeiro, Brazil. Not drawn to scale. Drawings by G. Bracher, adapted from Duellman and Gray (1983).

ment necessary for the completion of larval life was the yolk in the intestines of the hatchlings (Duellman et al., 2011).

Free-living feeding tadpoles are known to exist in 23 species and presumed to exist in 3 other species of *Gastrotheca* (Table 7.2). All of these are members of the subgenera *Duellmania* and *Gastrotheca* and live at high elevations (mostly above 2000 m) in the Andes. All known tadpoles of the genus *Gastrotheca* develop in ponds and man-made aquatic features, such as drainage ditches. Most tadpoles of various species resemble one another and, therefore, are difficult to identify; in some cases, the identity of tadpoles was determined by allozyme electrophoresis or DNA and a comparison with that of adults.

All tadpoles of *Gastrotheca* have nearly globular bodies and robust caudal musculature, which (at midlength of the tail) is about the same height as the dorsal or ventral fin (Fig. 7.20). The body length is about 40% of the tadpole's total length. The snout is bluntly rounded in dorsal view, and rounded or inclined anteroventrally in profile. The spiracle is short and attached to the body; it is sinistral and ventrolateral in position, at about midlength of the body. The cloacal tube is also sinistral and attached to the ventral fin. The dorsal fin originates on the posterior part of the body or on the proximal edge of the caudal musculature. Little interspecific variation exits in these features (Table 7.2). The width of the oral disc is about one-third the greatest width of the body; the median part of the upper labium is bare, whereas elsewhere there are two rows of marginal papillae ventrally and one row laterally (Fig. 7.20). There are two upper and three lower rows of keratinized labial teeth; the second upper row and/or the first lower row are interrupted medially in most species. The keratinized beaks are moderately massive and serrate. Most of these tadpoles are dull gray, but some are tan with a greenish tinge, and others have longitudinal dark marks on the caudal musculature (noted in the individual species accounts in chapters 10–12).

Evolution of Reproduction and Development

By the dawning of the Cenozoic, some 55 million years ago, ancestral terranan-hemiphractid frogs had forsaken reproduction in aquatic environments; they had developed terrestrial eggs with direct development into froglets. Tadpoles had become a thing of the evolutionary past. Yet endogenous development required nutrients for the completion of development. Consequently,

Table 7.2 Characteristics of tadpoles of *Gastrotheca*. Abbreviations: DF = dorsal fin; H = body height; VF = ventral fin; W = body width

Species	Body length / total length	Body width / body height	Profile snout	Profile throat	Cloacal tube	Origin of dorsal fin	Heights of fins and musculature	Marginal papillae
G. aguaruna	39.9	W = H	rounded	convex	conical, transverse	gradually from caudal musculature	DF > VF > muscle	1 lateral, 2 ventral
G. argenteovirens	40.3	W > H	abruptly inclined	concave	conical, transverse	gradually from body	DF = VF > muscle	2 lateral, 2 ventral
G. aratia	37.6	W > H	rounded	convex	conical, transverse	gradually from caudal musculature	DF = VF > muscle	1 lateral, 2 ventral
G. aureomaculata	41.3	W = H	rounded	convex	conical, transverse	gradually from body	DF = VF < muscle	1 lateral, 1 ventral
G. chrysosticta	45.5	W > H	rounded	convex	conical, transverse	gradually from body	DF = VF = muscle	2 lateral, 1 ventral
G. espeletia	37.3	W > H	inclined	convex	conical, transverse	abruptly from body	DF = VF = muscle	2 lateral, 1 ventral
G. gracilis	40.4	W > H	rounded	convex	flask-shaped, diagonal	gradually from body	DF = VF > muscle	1 lateral, 2 ventral
G. lojana	44.1	W > H	rounded	convex	conical, diagonal	gradually from caudal musculature	DF > VF > muscle	1 lateral, 1 ventral
G. marsupiata	42.2	W > H	inclined	concave	conical, diagonal	gradually from caudal musculature	DF = VF < muscle	1 lateral, 1 ventral
G. monticola	42.9	W > H	rounded	convex	conical, diagonal	gradually from caudal musculature	DF > VF < muscle	2 lateral, 2 ventral
G. peruana	40.3	W > H	rounded	convex	conical, diagonal	gradually from caudal musculature	DF = VF < muscle	1 lateral, 2 ventral
G. phalarosa	44.8	W > H	inclined	concave	conical, transverse	gradually from caudal musculature	DF > VF < muscle	1 lateral, 1 ventral
G. piperata	37.5	W > H	inclined	concave	conical, transverse	gradually from caudal musculature	DF = muscle > VF	1 lateral, 1 ventral
G. pseustes	37.3	W > H	inclined	convex	conical, transverse	gradually from body	DF < muscle > VF	1 lateral, 1 ventral
G. psychrophila	38.3	W < H	inclined	convex	conical, transverse	abruptly from body	DF = VF > muscle	2 lateral, 2 ventral
G. riobambae	43.0	W > H	rounded	concave	conical, transverse	gradually from body	DF = VF < muscle	2 lateral, 2 ventral
G. ruizi	36.1	W > H	inclined	convex	conical, transverse	gradually from body	DF = muscle > VF	1 lateral, 1 ventral
G. trachyceps	39.7	W > H	inclined	concave	conical, transverse	gradually from body	DF = VF > muscle	2 lateral, 2 ventral

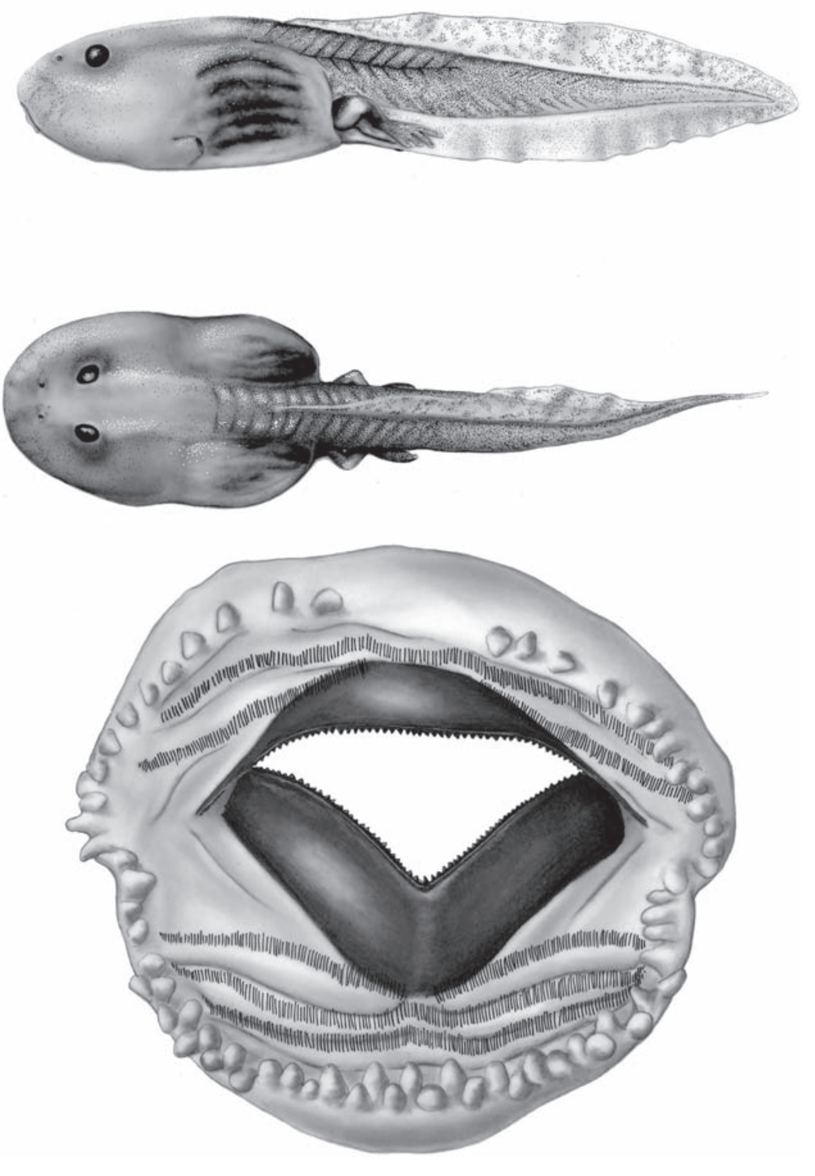

Fig. 7.20 Lateral and dorsal views and oral disc of the tadpole of *Gastrotheca peruana* (KU 215630), from 33 km NNW Cajamarca, 3490 m, Cajamarca, Peru. Total length = 62.0 mm. Drawings by G. Bracher.

female reproductive efforts changed from hundreds of eggs with minute amounts of yolk to a few eggs with large quantities of yolk. Also, the input of oxygen and the elimination of nitrogenous wastes, tasks easily accomplished via the egg membranes in the water, became a serious physiological problem on land. Embryos needed vascularized tissue next to the vitelline membrane for transport of oxygen and wastes. One group of these frogs developed a thin membranous tail that sufficed for a gaseous exchange with the environment; they deposited their eggs on the ground or adherent to leaves of bromeliads. These frogs underwent an explosive radiation in the Neotropics and came to be known as brachycephalids, ceuthomantids, craugastorids, eleutherodactylids, and strabomantids.

A second group solved the respiratory problem by developing a pair of gills, thin vascularized tissues adherent to the vitelline membrane and connected to the embryo by stalks with afferent and efferent blood vessels. As a way to protect eggs, which are left unprotected when on the ground, a novel pattern evolved. A male fertilized the few eggs that were produced and placed them on the back of the female. Thus, with the development of external gills and the evolution of male behavior—spreading sperm on the back of the female and using his feet to push each egg across

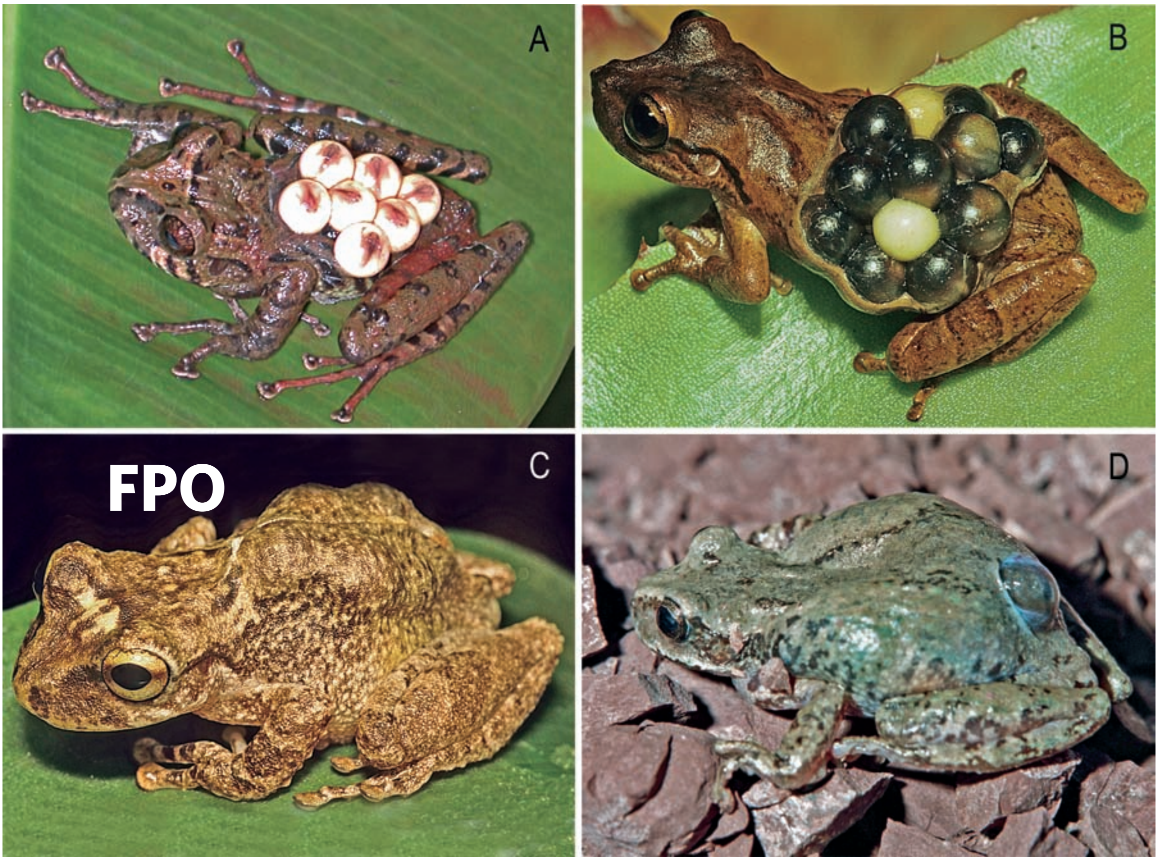

Fig. 7.21 Diversity of reproduction in hemiphractid frogs. A: eggs on the dorsum of *Stefania ayangannae*, from Mt. Kopinang, Guyana (note the blood vessels in the gill stalks and gills). B: eggs developing in an open basin on the back of *Fritziana goeldii*, from Rio de Janeiro, Brazil (note the two unfertilized eggs). C: embryos developing in a pouch with a middorsal slit-like opening in *Flectonotus pygmaeus*, from Ocumare–de la Costa road, Aragua, Venezuela. D: direct development in a closed pouch of *Gastrotheca christiani*, from Parque Nacional Callilegua, Jujuy, Argentina (note the protruding hatchling). Photos by D. B. Means (A), K.-H. Jungfer (B and C), and M. Vaira (D), KUDA.

the sperm and onto the back of the female—a new lineage was born, Hemiphractidae. The maintenance of this mode of reproduction led to other morphological, physiological, and behavioral adaptations that are unique to this lineage.

The female, toting around a couple dozen eggs on her back, could easily loose some eggs. This problem was solved by the production of a mucus layer on the back, to which the eggs could adhere. This mode of development exists to the present in members of the genera *Cryptobatrachus*, *Hemiphractus*, and *Stefania* (Fig. 7.21A). Eggs that were naked on the female's back were subject not only to desiccation, but also to predation by yolk-sucking wasps and flies. This dilemma was solved independently in three lineages. In the humid coastal forests of what is now southeastern Brazil, females developed dermal ridges on their backs, forming basin-like structures that contained the eggs, which hatched before metamorphosis was completed (Fig. 7.21B). The advanced tadpoles survived in water-filled cavities in plants. Although they were capable of feeding, they could complete their metamorphosis by utilizing the yolk in their intestines. Meanwhile, far to the north in what is now coastal Venezuela, another group of small frogs, the females of which were burdened by only a few large eggs developing in a pouch-like structure formed by longitudinal folds that met middorsally, deposited their advanced tadpoles in bromeliads (Fig. 7.21C). These tadpoles completed their metamorphosis solely by utilizing the yolk in their intestines.

While these kinds of modification in the frogs' reproductive mode were going on, another important morphological change took place. In the most basal hemiphractids (*Cryptobatrachus* and *Flectonotus*), respiration was accomplished by a single pair of small gills. More effective respiration occurred through the development of a second pair of gills, which became far more extensive and eventually fused; these gills completely encased the embryo and yolk. Upon hatching, the gills were sloughed off as the froglet breathed by means of lungs.

Egg transport and protection were further advanced by the formation of a permanent pouch on the back of the female in those taxa now recognized as marsupial frogs of the genus *Gastrotheca*. After the male exudes sperm between the cloaca and the opening of the pouch, some eggs may roll from the uplifted cloaca to the pouch; males learned to use their hind feet to move the eggs and direct them into the pouch. This was facilitated by a dermal ridge leading to a large opening in a pouch with a median membrane. The pouch was not simply a pocket. Instead, immediately upon the entrance of eggs, membranous filaments containing capillaries arose from the lining of the pouch, thereby ensuring a source of oxygen for each developing embryo. Upon hatching, the young could either simply crawl out of the pouch or be extruded, still possessing their gills (Fig. 7.21D). Those that remained in the pouch were dug out by the female's vigorous use of her feet.

In western South America, crustal movements built one of the most massive mountain ranges in the world, the Andes; for millions of years, the mountains rose higher and higher (chapter 8). On windward slopes of these mountains, the forests were continuously moistened by rain and dew from clouds, an ideal habitat for frogs of many kinds, including marsupial frogs. These latter frogs could spend their entire lives in the trees. Life in bromeliads was enhanced by brood pouches that expanded laterally, so eggs developed on the flanks of the female instead of on her back, thereby allowing the frog to squeeze between the leaves. In one lineage, the pouches were lateral and then entered the body cavity, so eggs developed within the coelomic cavity.

Some marsupial frogs ventured into the puna or páramo, treeless areas at high elevations. They lived on the ground but would crawl up small bushes at night; otherwise they maintained the life of a marsupial frog in the cloud forest. But one strain took on a new way of life; they retraced their evolutionary path and created more and smaller eggs that hatched as tadpoles, which were placed in ponds to undergo an exogenous development. These tadpole-producing marsupial frogs speciated in the high Andes; in some cases they reentered the cloud forests and returned to producing froglets instead of tadpoles.

Thus hemiphractids took on a new way of reproducing. This was not a sole evolutionary event, but a series of correlated morphological and physiological changes that prompted behaviors unknown in any other frogs. These changes culminated in *Gastrotheca*, a genus truly deserving the name marsupial frogs.

Gastrotheca is the only genus of frogs in which phylogenetic evidence points to reversals in the mode of their life history. The "re-evolution" of aquatic larvae within taxa having direct development is also known in the plethodontid salamander genus *Desmognathus* in eastern North America (Chippendale et al., 2004; Chippindale and Wiens, 2005) and in the ancestral stock for three genera of indotyphlid caecilians in the Seychelles Islands (Mauro et al. 2014). In these cases the evolutionary change is unidirectional, whereas in some "re-evolved" lineages of *Gastrotheca*, there is a return to their ancestral state (chapter 3).

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8

Biogeography

Herein I provide a brief synopsis of that part of the geological and climatic history of South America that pertains to the history of hemiphractid frogs. Thereafter I attempt to interpret the evolutionary history of the marsupial frogs and their allies. Lastly I discuss the present distributions of these frogs.

History of South America

In the Early to Middle Cretaceous, around 100–90 million years ago (mya), western Gondwanaland was divided by a narrow water body, the proto-Atlantic Ocean. Thus began the isolation of a large island continent, South America, from the rest of Gondwanaland. After its separation from Africa in the Cretaceous and from the Antarctic-Australian landmass in the Middle Oligocene, it was isolated until its connection with North America via Panama in the Pliocene (Pittman et al., 1993). Throughout the later Cretaceous and the Cenozoic, the continent underwent major geological transformations and witnessed dramatic climate changes. The basement rocks of the Guianan and Brazilian Shields (Fig. 8.1) are Precambrian (Almeida et al., 1973). The two regions may have been continuous with one another until the Late Cretaceous, when both were elevated, and a major embayment of the Atlantic Ocean separated these ancient formations until the Late Miocene. Both shields were uplifted farther in the Tertiary (Beurlen, 1970; Valeton, 1973).

Further uplift of the Brazilian Shield must have occurred during the Cenozoic, because most of the shield above 1200 m is covered with Cretaceous sediments (Freitas, 1951). He recognized three major uplifts and suggested that the first of these was at the end of the Cretaceous, with the other two in the Tertiary, when the Serra do Mar, Serra da Mantiqueira, and associated ranges were fully formed, although their origins date back to the Late Cretaceous, when they were created by arching and fracturing of the ancient shield along northeast–southeast lines.

The Guiana Shield has basement igneous and metamorphic rocks of Proterozoic age, which have a thick layer of sandstone (Roraima Formation) deposited about 1.5–1.8 billion years ago (Ghosh, 1985). According

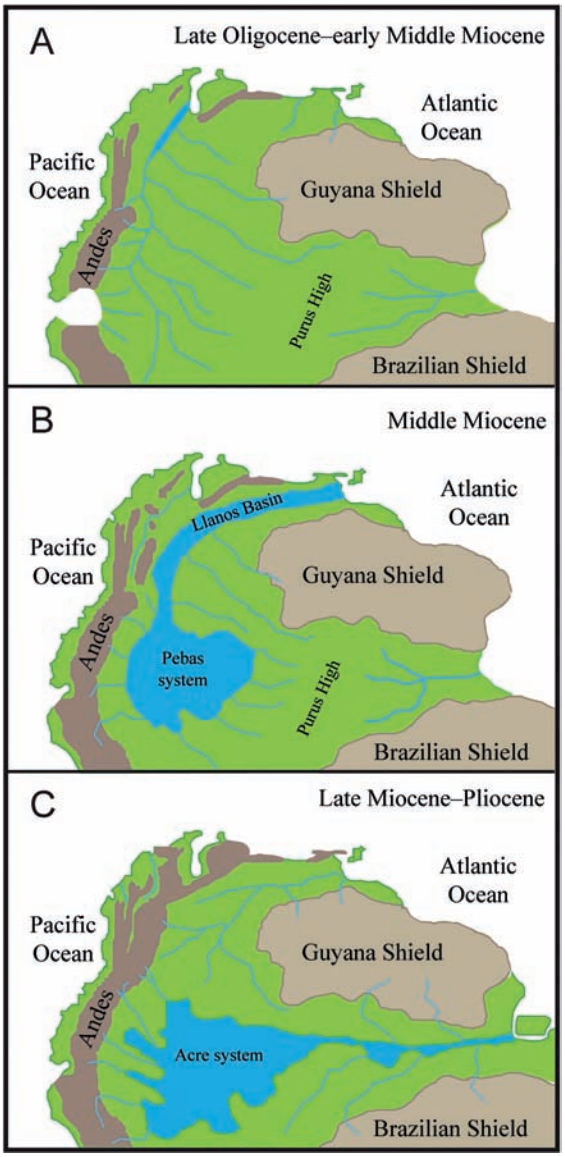


Fig. 8.1 Generalized paleogeographic maps of northern South America. Maps modified from Hooghiemstra and van der Hammen (1998) and Wesselingh and Hoorn (2011).

to Gansser (1954), the Guiana Highlands were uplifted in the Early Cretaceous, if not sooner (Oliveira and Leonardos, 1943). Schubert and Briceño (1987), on the other hand, postulated that the first uplift was in the Proterozoic, followed by three other periods of uplift: Mesozoic, Paleocene, and later Tertiary. The present table mountains (tepuis) are erosional remnants of the Cretaceous uplifts (Haffer, 1974). Most tepuis have flat tops and perpendicular cliffs (300–1000 m high) that separate the tops from the talus slopes below.

A variety of geological evidence (Hoorn et al., 1995; Hoorn, 2006; Mora et al., 2010) shows that despite modest elevation of the Andes as early as the Late Cretaceous, the major drainage of what is now the Amazon Basin was westward into the Pacific Ocean at about what today is the Gulf of Guayaquil. The Andes underwent major tectonic events in the Early to Middle Miocene (± 14 mya) that resulted in the drainage shifting eastward and emptying into the Atlantic Ocean. During the Miocene and Pliocene, large marine embayments and freshwater lakes presided in what is now the Amazon Basin. Shortly after the elevation of the Andes in the Early to Middle Miocene, the basin was drained primarily by the precursor of the Río Orinoco, which flowed into the Caribbean Sea. In the Late Miocene to Early Pliocene, the present drainage via the Río Amazonas to the Atlantic Ocean was established (Fig. 8.1). The current Amazon Basin covers about 8 million square kilometers, and the Amazon River is about 6400 km long from its source in the Peruvian Andes to its mouth in northeastern Brazil (Sioli, 1984).

As the South American Plate arced northwestward for millions of years, it encountered the Nazca Plate. The ongoing subduction of the Nazca Plate under the South American Plate is largely responsible for the orogenic events resulting in the rise of the Andes, the dominant physiographic feature in western South America. A major structural deflection of the Andes exists in what is now southern Ecuador and northern Peru, This is the Huancabamba Deflection, physiographically referred to as the Huancabamba Depression. There are significant differences in the origins of the mountains to the south of the depression (the central Andes) and those north of the depression (the northern Andes).

The uplifted terrain that resulted from the Late Cretaceous orogeny south of the Huancabamba Depression had been eroded into low hills by the beginning of the major uplift in the Miocene. The Cordillera Occidental was only about half of its present height 25–10 mya, and the Cordillera Oriental and the Altiplano also were about half of their present height 10 mya (Gregory-Wodzicki, 2000). The last major uplift was in the Pliocene; some additional orogenies took place in the Pleistocene (Jaillard et al., 2000). Parts of the Cordillera Oriental and the Altiplano were uplifted to their present heights during the last 10 million years (Gregory-Wodzicki, 2000).

In contrast to the central Andes, the northern Andean Cordillera had a more complex and mostly later history. In the Late Cretaceous the northern Andes were uplifted to elevations probably no higher than 1000 m

(Zeil, 1979). According to Galvis and Mojica (1993), in the Early Tertiary an island arc west of the present Cordillera Occidental extended from Panama to northern Ecuador. This land mass contributed to the mountains in western Colombia and extreme northwestern Ecuador. The major uplift of the Andes north of the Huancabamba Depression was initiated in the Late Miocene and Pliocene and continued into the Quaternary, as evidenced by numerous active volcanoes in Colombia and Ecuador. This timing is supported by palynological data showing that high elevations (above 2000 m) in the Cordillera Oriental in Colombia were reached in the Middle to Late Pliocene (van der Hammen, 1974). Orogenic events beginning in the Miocene were instrumental in the formation of major drainage systems, such as that of the Río Magdalena (Hoorn et al, 1995). This river and the Río Cauca separate the Andes in Colombia into three north–south ranges: the Cordillera Occidental, Cordillera Central, and Cordillera Oriental.

The Mérida Andes in Venezuela are distinct from the main chain of the Andes to the west. Uplift of the Mérida Andes began in the Oligocene (Shagam, 1975) and continued into the Quaternary; during the Late Miocene and Early Pliocene the uplift of the Mérida Andes was congruent with that of the Cordillera Oriental. The low Táchira saddle separates the two cordilleras. The Cordillera de la Costa was also uplifted in the Oligocene but has not been uplifted since then (Liddle, 1946). The Sierra Nevada de Santa Marta, the northernmost mountains that are completely removed from the principal cordilleras, may have been uplifted as late as the Pleistocene (Gansser, 1955).

Pleistocene glaciation and its accompanying climatic shifts took place in the South American highlands (especially in the Andes), just as they did in the Northern Hemisphere. The Brazilian Highlands have few mountains exceeding elevations of more than 2500 m; the highest is Pico do Itatiaia (2822 m) in the Serra Mantiqueira. The extent of glaciation there, if any, is questionable, although Ebert (1960) suggested that the presence of large boulders and U-shaped valleys were the result of glaciation on Itatiaia. Glaciation has not been documented in the Guiana Highlands.

A considerable amount of data reveal glacial phenomena in the northern Andes (Vuilleumier, 1971; Simpson, 1975). The extensive palynological record in Colombia shows that the Recent vegetation of the high Andes did not exist before the Late Pliocene (van der Hammen, 1974; van der Hammen and Hooghiemstra, 1997), These data suggest a 6°C–7°C drop in temperature during glacial maxima in the highlands, whereas the drop in temperature was only about 3°C in the lowlands (Haffer, 1979; Fig. 8.2). Likewise, carbon 14 dating of oxygen isotopes and dust particles in ice cores from three Andean glaciers—Nevado Huascarán (6046 m) and the Quelccaya Ice Cap (5670 m) in Peru, and Volcán Sajama (6542 m) in Bolivia—show changing climatic conditions in the Andes during the past 25,000 years (Thompson et al., 1995, 1998, 2006). According to Simpson (1979), major glaciations occurred about 250,000 and 130,000 years ago, and the last minor glacial advance took place only about 14,000 years ago.

An important aspect of the glacial period is the elevational shift in climates and in their associated vegetation. Climatic compression was addressed by Duellman (1983), who applied an adiabatic lapse rate to the compression of vegetation zones in the Andes. Because moist air cools more slowly than dry air, adia-

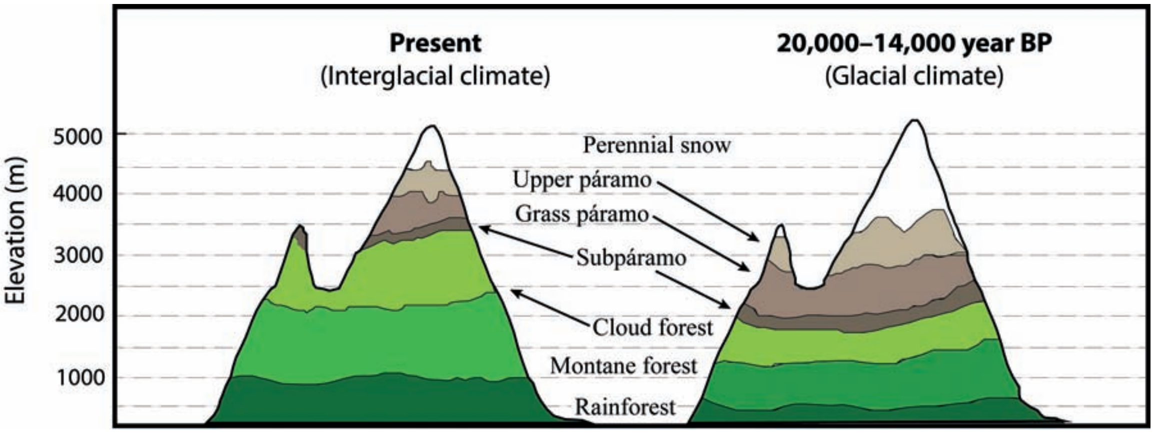


Fig. 8.2 Diagrammatic cross-section of the Andes at the latitude of Bogotá, Colombia, showing vegetation zones at the Last Glacial Maximum and the present. Presentation by Hooghiemstra et al. (2006), as modified from van der Hammen (1974).

batic lapse rates range from a loss of 6°C per 1000 m of elevation for saturated air to a loss of 10°C per 1000 m of elevation for dry air. This type of compression was applied to the Andes in western Ecuador by Lynch and Duellman (1997).

Two other chronological events need to be addressed. Although not pertaining to the speciation of marsupial frogs, the connection of North America and South America in the Late Pliocene (± 5.7 mya) allowed dispersal of two genera of hemiphractid frogs into Central America (Duellman, 1979). Also, the continental islands of Trinidad and Tobago have the same geology as the coastal ranges of Venezuela; they are a continuation of the Península de Paria, from which Trinidad is separated by only 11 km of water less than 40 m in depth (Murphy, 1997).

Evolutionary History of Hemiphractidae

As emphasized by Báez et al. (2012), a diversity of hyloid neobatrachians within the unranked taxon Noblebatrachia existed in South America in the Late Cretaceous. Unfortunately, none of these is a hemiphractid, so the temporal placement of *Gastrotheca* and its relatives lies on indirect evidence. A timetree based on a Bayesian analysis of sequences of nine genes (Heinicke et al., 2009) showed the time of divergence of Hemiphractidae from the unranked taxon Terrarana to be 64.9 mya, with a credibility interval of 87.7–46.5 mya. This was used as the basis for a timetree of Hemiphractidae.

According to the temporal estimates shown in Figure 8.3, all of the genera of hemiphractids may have diverged before the end of the Eocene, but the last divergence, *Gastrotheca*, may have been in the Early Oligocene. The divergence of *Cryptobatrachus* and *Flectonotus* supposedly took place in the Middle Eocene, but it may have occurred any time between the Early Paleocene and the Early Miocene. Both genera inhabit mountains in northwestern South America. *Flectonotus* may have diverged from *Cryptobatrachus* at the time of the Oligocene uplift of the Cordillera de la Costa and Cordillera Paria, where members of this genus live today. Ancestral *Cryptobatrachus* could have been widespread in Colombia prior to the rise of the three cordilleras and the Sierra Nevada de Santa Marta, all of which are highlands inhabited by species of *Cryptobatrachus* today.

Hemiphractus also diverged from its ancestral stock in the Middle Eocene, with a credibility interval from the Cretaceous–Cenozoic boundary to the Early Miocene. Most species inhabit the upper Amazon Basin, but *H. bubalus* differentiated from *H. proboscideus* in the Late Miocene and ascended the Cordillera Oriental as this set of mountains began to rise in the Late Miocene. Even earlier, in the Middle Miocene, *H. fasciatus* differentiated from *H. helioi*; subsequently, the former became isolated on the Pacific versant and eventually expanded its range into Panama.

The ancestor to *Stefania* and *Fritziana* must have inhabited the eastern parts of the Guiana Shield and the Brazilian Shield before the drainage of the Amazon Basin shifted to its present position in the Middle Miocene. The timetree shows the divergence of *Stefania* and *Fritziana* to be in the Late Eocene, with credibility intervals being from the Middle Paleocene to the Early Miocene. Speciation in *Fritziana* in the mesic region of southeastern Brazil occurred during the last 10 million years. Most biologists (e.g., Chapman, 1931; Maguire, 1970; Hoogmoed, 1979; McDiarmid and Donnelly, 2005) determined that speciation occurred during the erosion of the Cretaceous sandstones and that the inhabitants of the isolated tepuis were relicts of past widespread species. The timing of speciation among *Stefania* and other inhabitants of the tepuis in the Guiana Region was challenged by Kok et al. (2012) and Salerno et al. (2012). Their analyses of sequence data of several genera of anurans show conclusively that speciation took place in the Pliocene. Thus these frogs dispersed from summits of tepuis long after their formation. The timing of differentiation among species of *Stefania* shown in Figure 8.3 is from the Middle Miocene to Early Pliocene and is supportive of the timing presented by Kok et al. (2012) and Salerno et al. (2012).

The historical biogeography of the basal groups of *Gastrotheca* does not conform to past or present geological or climatic events. *Gastrotheca* is most speciose in northwestern and Andean South America. There are two clades in eastern and southeastern Brazil, but no species in the intervening Guiana Shield or the Amazon Basin. The only other group of frogs having a somewhat similar pattern of distribution is Centrolenidae (Guayasamin et al., 2009). Like *Gastrotheca*, the greatest differential of centrolenids is in the tropical Andes, with a minor differentiation in the highlands in southeastern Brazil, but there are centrolenids in the northern Amazon Basin and in the Guiana Region. Presumably *Gastrotheca* originated in the Early Oligocene (± 32 mya). Shortly thereafter it dispersed throughout the humid forests in northwestern South America, through the Guiana Region (where it is now extinct), and into eastern and southeastern Brazil. During the period from the Late Oligocene to the Middle Miocene, the ancestral *Gastrotheca* differentiated into

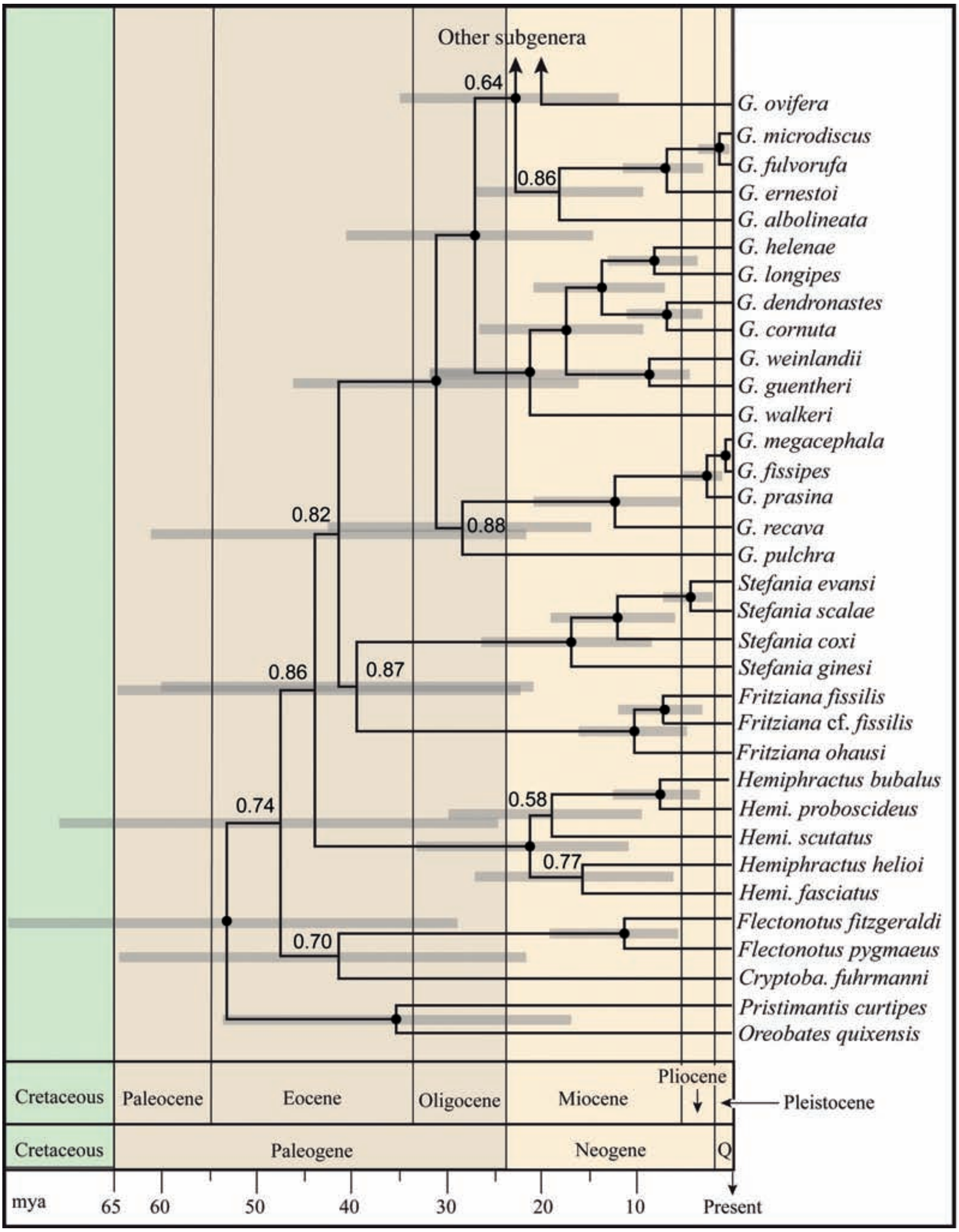
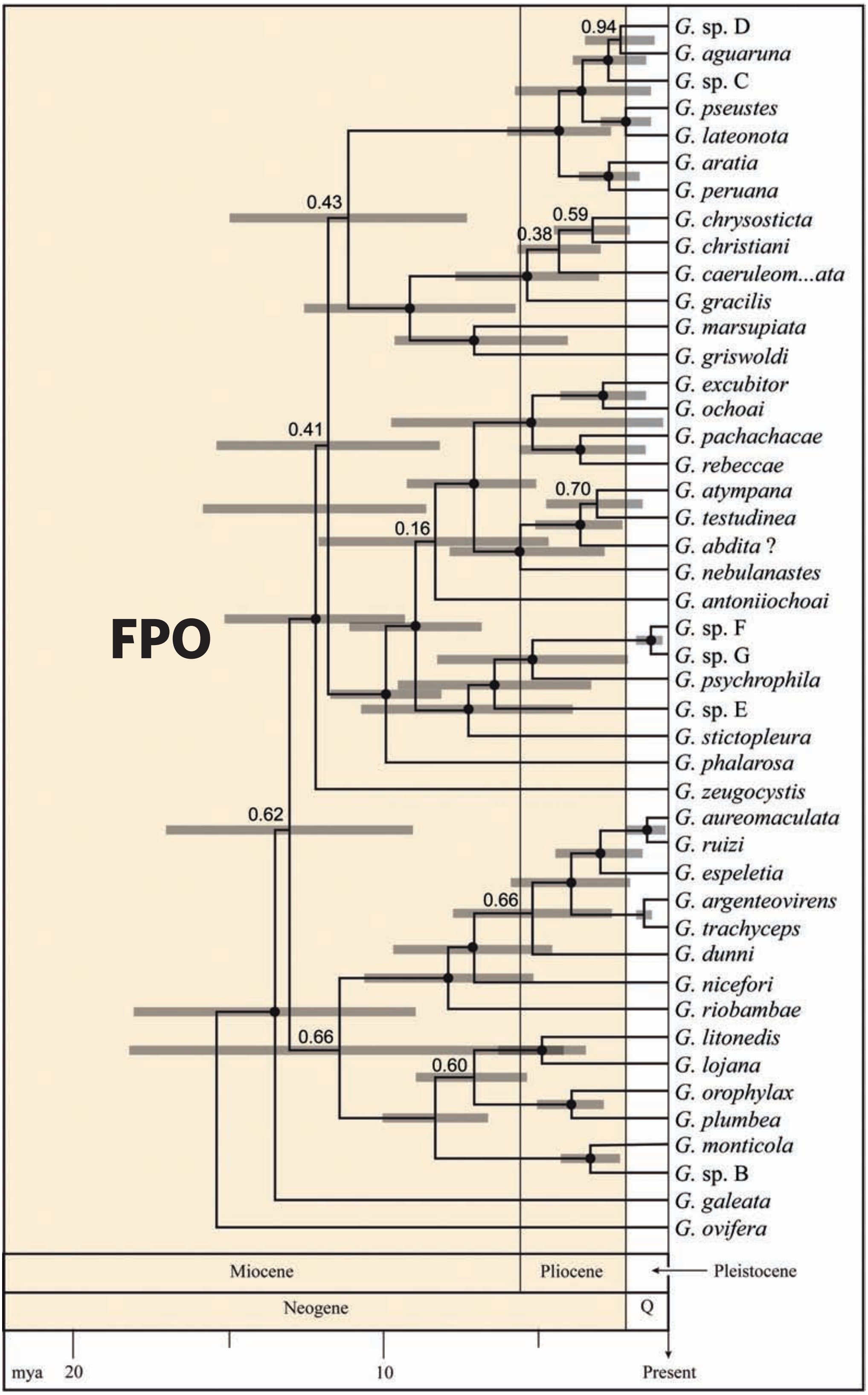

Other subgenera
0.64
0.86
0.82
0.88
0.86
0.87
0.74
0.58
0.77
0.70
G. ovifera
G. microdiscus
G. fulvorufa
G. ernestoi
G. albolineata
G. helenae
G. longipes
G. dendronastes
G. cornuta
G. weinlandii
G. guentheri
G. walkeri
G. megacephala
G. fissipes
G. prasina
G. recava
G. pulchra
Stefania evansi
Stefania scalae
Stefania coxi
Stefania ginesi
Fritziana fissilis
Fritziana cf. fissilis
Fritziana ohausi
Hemiphractus bubalus
Hemi. proboscideus
Hemi. scutatus
Hemiphractus helioi
Hemi. fasciatus
Flectonotus fitzgeraldi
Flectonotus pygmaeus
Cryptoba. fuhrmanni
Pristimantis curtipes
Oreobates quixensis
Cretaceous
Paleocene
Eocene
Oligocene
Miocene
Pliocene
Pleistocene
Cretaceous
Paleogene
Neogene
Q
mya
65
60
50
40
30
20
10
Present

Fig. 8.3 Generalized timetree of hemiphractid frogs. Gray bars represent Bayesian credibility intervals. Numbers at the nodes are Bayesian posterior probabilities; black dots are probabilities of 95% or more.

several clades: *Eotheca* in eastern Brazil, *Australotheca* in southeastern Brazil, *Amphignathodon* in northwestern South America, and *Cryptotheca* and *Opisthodelphys* in the coastal mountains in northern Venezuela.

The ancestral stock of the Andean subgenera *Duellmania* and *Gastrotheca* originated in the Middle Miocene (± 13 mya). Differentiation of species of *Gastrotheca* in the central Andes mostly occurred in the Late Miocene and Pliocene, whereas most of the divergence of species of *Duellmania* in the northern Andes took place in the Pliocene and Pleistocene. This difference in their times of speciation is concordant with the earlier uplift of the Andes south of the Huancabamba Depression.


G. sp. D
G. aguaruna
G. sp. C
G. pseustes
G. lateonota
G. aratia
G. peruana
G. chrysosticta
G. christiani
G. caeruleom...ata
G. gracilis
G. marsupiata
G. griswoldi
G. excubitor
G. ochoai
G. pachachacae
G. rebeccae
G. atympana
G. testudinea
G. abdita ?
G. nebulanastes
G. antoniiochoai
G. sp. F
G. sp. G
G. psychrophila
G. sp. E
G. stictopleura
G. phalarosa
G. zeugocystis
G. aureomaculata
G. ruizi
G. espeletia
G. argenteovirens
G. trachyceps
G. dunni
G. nicefori
G. riobambae
G. litonedis
G. lojana
G. orophylax
G. plumbea
G. monticola
G. sp. B
G. galeata
G. ovifera
0.94
0.43
0.59
0.38
0.41
0.70
0.16
0.62
0.66
0.66
0.60
FPO
Miocene
Pliocene
Pleistocene
Neogene
Q
mya
20
10
Present

Present Distributions

With the exception of *Gastrotheca*, the distributions of most of the genera of hemiphractids are restricted to specific physiographic regions (see maps in chapter 9). *Cryptobatrachus* is confined to moderate elevations in the northern Andes, and *Flectonotus* has a discontinuous distribution at moderate elevations in northern Venezuela and adjacent Trinidad and Tobago. Populations of most species of *Stefania* exist on isolated table mountains in the Guiana Region, and *Fritziana* is dispersed in lowlands to moderate elevations in southeastern Brazil. *Hemiphractus* inhabits tropical rainforest in the Amazon Basin and on Pacific lowlands of northwestern South America, as well as humid montane forests on the slopes of the Andes.

As noted above, a great hiatus exists between the major portion of *Gastrotheca* in western South America and the 10 species in eastern Brazil (Fig. 9.11). Two of the "western" subgenera, *Cryptotheca* and *Opisthodelphys*, have disjunct distributions in the Cordillera de la Costa and the Sierra de Aroa in northern Venezuela. With the exception of the high-Andean *G. helenae*, all species in the subgenus *Amphignathodon* occupy forested slopes of the Andes and adjacent lowlands. Of these, only *G. longipes* inhabits the Amazon Basin; nearly all localities from where it is known are within sight of the Andes.

Most of the species of *Gastrotheca*, including all species in the subgenera *Duellmania*, *Edaphotheca*, and *Gastrotheca*, occur in the Andes from northern Colombia to northern Argentina (Fig. 8.4). Latitudinal distributions are short for most species, but *G. testudinea* is found at elevational ranges of 1100–1775 m from Ecuador to Bolivia. At higher elevations, *G. marsupiata* and *G. peruana* also are exceptions; both have north–south ranges exceeding 1000 km, at elevations mostly above 2500 m. Geographic and elevational ranges of some species are extremely limited, inasmuch as some species (e.g., *G. carinaceps*, *pacchamama*, and *zeugocystis*) are known only from a single locality. *G. monticola* has the greatest range in elevation, from 1000 to 3350 m.

All of the 11 species known from elevations below 2000 m inhabit forests, and 3 of them (*Gastrotheca christiani*, *chrysosticta*, and *gracilis*) are from the southernmost localities in northwestern Argentina. Thirty species occur at elevations of 2500–3000 m, and 15 of those are among the 30 species known from elevations of 3000–3500 m. Only 5 species occur at elevations above 3500 m, all of which exceed 4000 m. The highest elevation from which any *Gastrotheca* is known is 4360 m (*G. peruana*). As shown in Figure 8.4, there is no

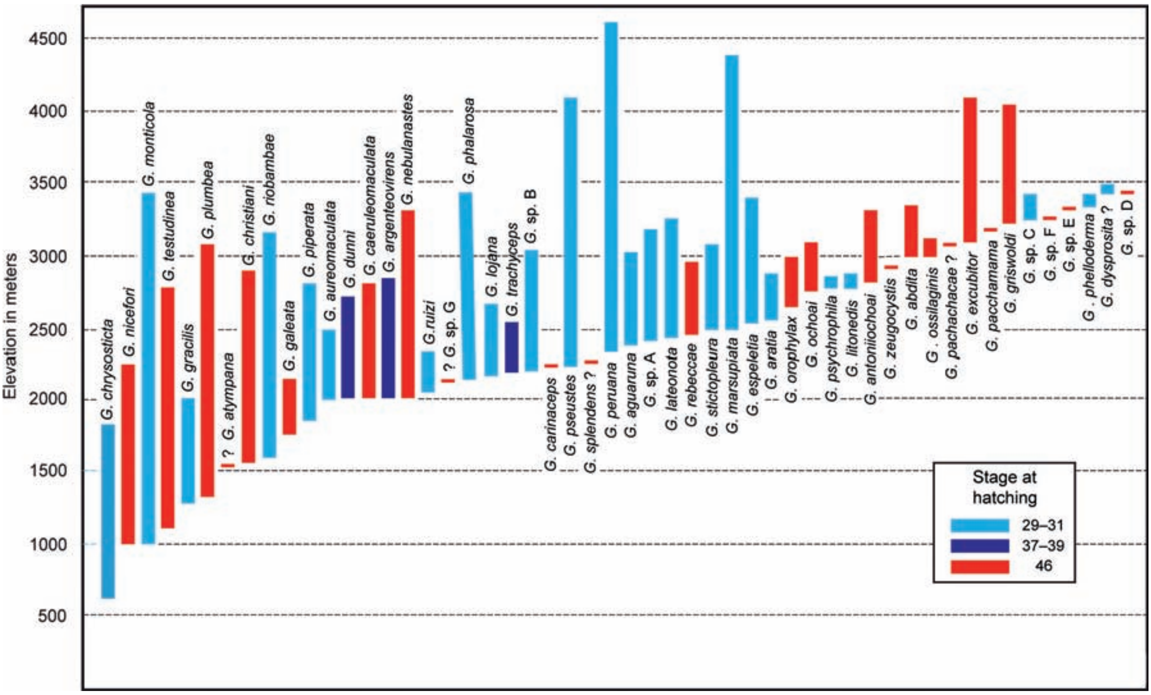


Fig. 8.4 Elevational distributions of species of *Gastrotheca* in the Andes, with notations of the stages at hatching.

elevational distinction between species having direct development and those having tadpoles.

Gastrotheca nicefori (as the taxon is now recognized) has the greatest geographical distribution in the genus. This species occurs at elevations of 1140–2265 m in the Andes in Colombia, and it has descended to disperse into the Serranía de Macarena (to the east of the Andes) in Colombia and the Mérida Andes in Venezuela, where it is known from elevations of 400–1600 m in the former and 1300–1750 m in the latter. *G. nicefori* also has dispersed into Central America, where it is known from several localities at elevations of 860–1699 m in Panama. Two other species of hemiphractids have dispersed into Central America: *G. cornuta* through Panama and into Costa Rica, and *Hemiphractus fasciatus* to western Panama. It is surprising that *G. nicefori* does not occur in the Sierra Nevada de Santa Marta. No species of *Gastrotheca* is known from that isolated mountain range in northern Colombia, but *Cryptobatrachus* does occur there.

Habitats of Hemiphractid Frogs

As might be expected, frogs ranging from Costa Rica to northwestern Argentina and southeastern Brazil, and extending from sea level to elevations in excess of 4000 m, inhabit extremely different environments. Herein I discuss and illustrate the habitats of hemiphractid frogs, nearly every species of which is restricted to one type of vegetation.

The Amazon Basin contains the largest tropical rainforest in the world; it is the largest biogeographic region in South America. Together with the adjacent Guiana Region, the Amazon Basin encompasses roughly 6 million square kilometers and is home to about 350 species of amphibians (Duellman, 1999). Nonetheless, hemiphractid frogs are poorly represented in the Amazon Basin; they occur only in the western part of the basin, where the climate is aseasonal and supports classic tropical rainforest (Fig. 8.5) inhabited by *Gastrotheca longipes* and three species of *Hemiphractus* (*H. helioi*, *proboscideus*, and *scutatus*). On the lower slopes of the Andes and in the highlands in Central America, the tropical lowland rainforest changes into the humid montane forest (Fig. 8.6). Some species, such as *G. cornuta* and *H. fasciatus*, ascend into humid montane forests in Central America and on the Pacific slopes of the Andes in Colombia.

At elevations above 1000 m to as high as 2800 m on the mountains in tropical western South America, condensation from heavy, usually daily clouds provide an idyllic habitat for frogs of many genera (Fig. 8.7). Frogs having direct development especially utilize this humid habitat. Thus cloud forests contain a large number of craugastorid *Pristimantis* and, of the 25 species of *Gastrotheca* in this habitat, 23 have direct development. Cloud forests also are inhabited by *Flectonotus pygmaeus* and *Hemiphractus bubalus*. The southernmost species of *Gastrotheca* (*G. christiani*, *chrysosticta*, and *gracilis*) in the Andes of Argentina inhabit subtropical and mesic forests at elevations of 600–2600 m (Fig 8.8).

The Atlantic Coast Forest occupies slightly more than 1 million square kilometers and has a large anuran fauna, of which more than 92% are endemic (Duellman,

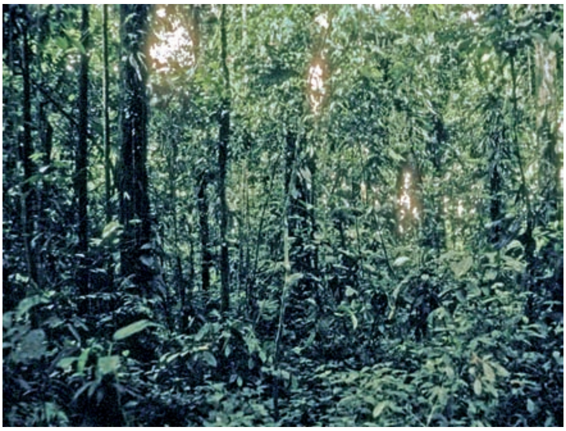


Fig. 8.5 Interior of a lowland tropical rainforest at Santa Cecilia, 340 m, Sucumbíos, Ecuador, November 1966. Habitat of *Hemiphractus proboscideus*. Photo by W. E. Duellman.

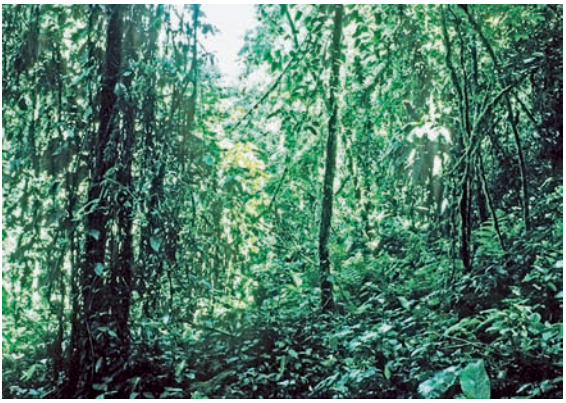


Fig. 8.6 Humid montane forest at Río Claro, 910 m, N slope Cerro Pando, Bocas del Toro, Panama, May 1966. Habitat of *Gastrotheca cornuta* and *Hemiphractus fasciatus*. Photo by W. E. Duellman.

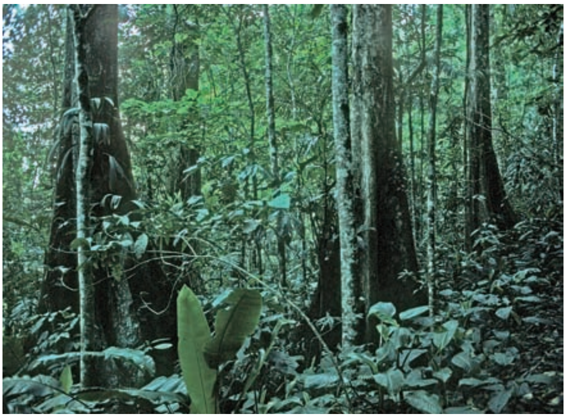


Fig. 8.7 Cloud forest in the Parque Nacional Henri Pittier, 1100 m, Aragua, Venezuela, August 1974. Habitat of *Flectonotus pygmaeus*, *Gastrotheca ovifera*, and *G. walkeri*. Photo by W. E. Duellman.

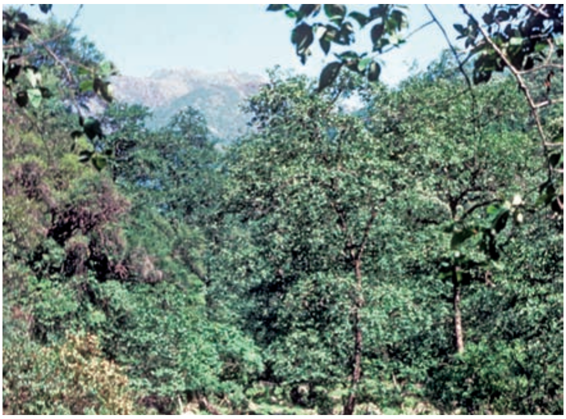


Fig. 8.8 Mesic forest, 1600 m, 21 km SSE Tafí del Valle, Tucumán, Argentina, December 1974. Habitat of *Gastrotheca gracilis*. Photo by W. E. Duellman.

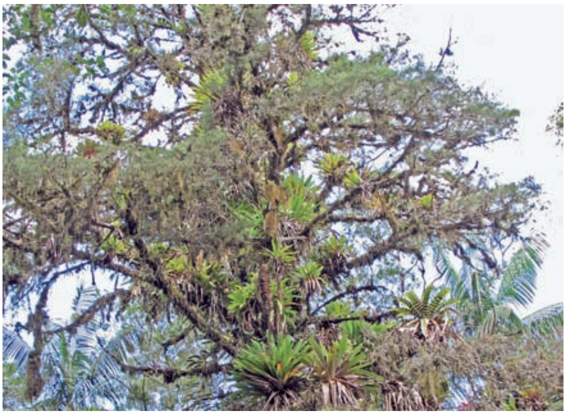


Fig. 8.9 Bromeliad-laden trees in the Atlantic Coastal Forest at Boraceia, 800 m, São Paulo, Brazil, July 2011. Habitat of various species of *Gastrotheca*. Photo by W. E. Duellman.

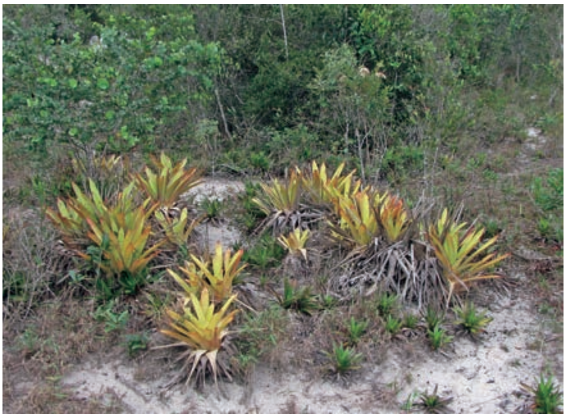


Fig. 8.10 Terrestrial bromeliads in Jequitinhonha municipality, Minas Gerais, Brazil, December 2009. Habitat of *Gastrotheca prasina*. Photo with permission granted by the photographer, M. Teixeira Jr.

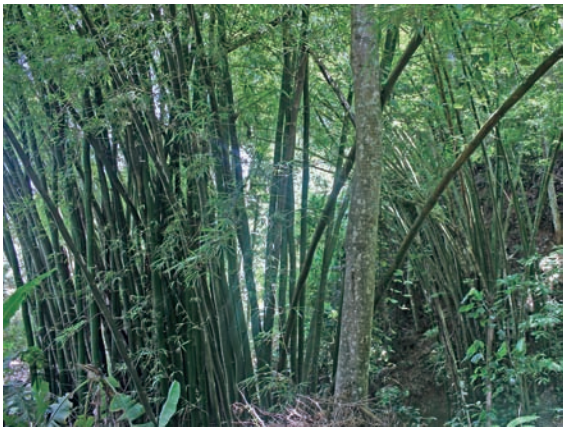


Fig. 8.11 Bamboo forest at Santa Teresa, Espírito Santo, Brazil, January 2014. Habitat of *Fritziana ohausi*. Photo with permission granted by the photographer, M. Folly.

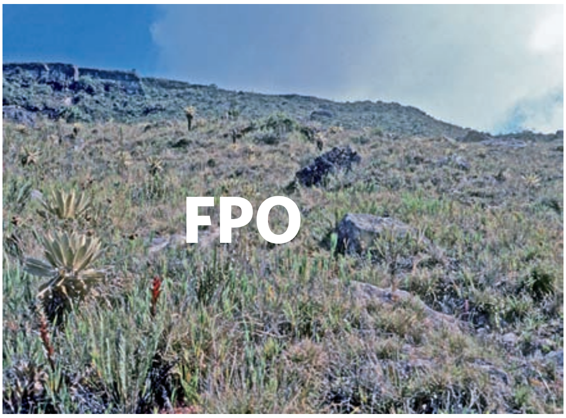


Fig. 8.12 Páramo near the crest of Cerro Tamá, 3000 m, Táchira, Venezuela, January 1979. Habitat of *Gastrotheca helenae*. The broad-leafed plants are *Espeletia*. Photo by W. E. Duellman.

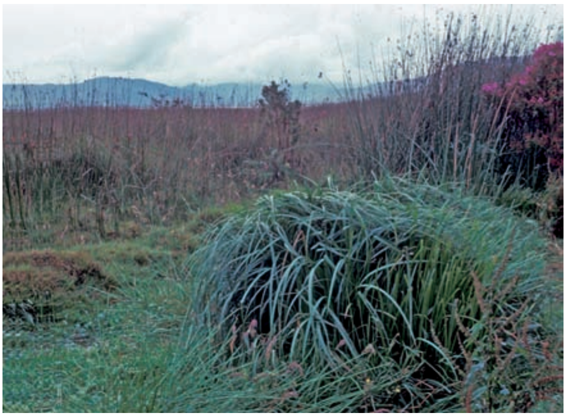


Fig. 8.13 Marsh at the edge of Lago de la Cocha, 2790 m, Nariño, Colombia, September 1974. Habitat of *Gastrotheca espeletia*. Photo by W. E. Duellman.

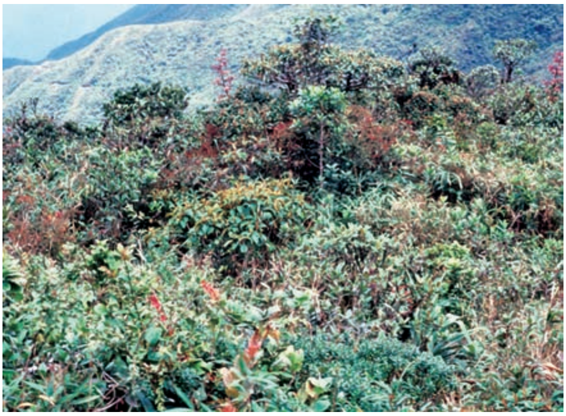


Fig. 8.14 Subpáramo with large terrestrial bromeliads at Abra de Zamora, 2850 m, Loja, Ecuador, March 1975. Habitat of *Gastrotheca psychrophila*. Photo by W. E. Duellman.

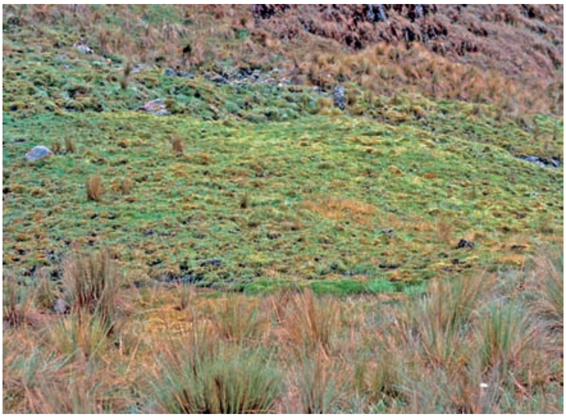


Fig. 8.15 Humid puna with mosses and a bunchgrass (*Stipa*) at Abra Málaga, 4120 m, Cusco, Peru, January 1977. Habitat of *Gastrotheca excubitor*. Photo by W. E. Duellman.

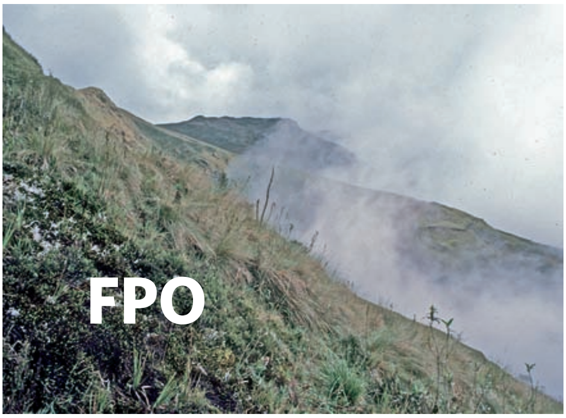


Fig. 8.16 Fog-enshrouded puna, N slope Abra Barro Negro, 3440 m, Amazonas, Peru, January 1989. Habitat of *Gastrotheca dysprosita*. Photo by W. E. Duellman.

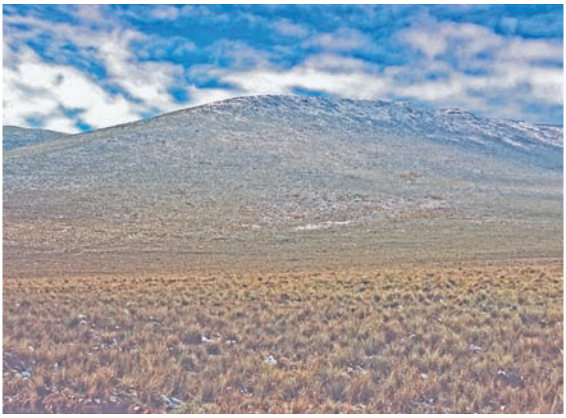


Fig. 8.17 Dry puna with a bunchgrass (*Stipa*) in the Pampas de Junín, near Carahuamayo, 4080 m, Junín, Peru, January 1971. Habitat of *Gastrotheca griswoldi*. Photo by W. E. Duellman.

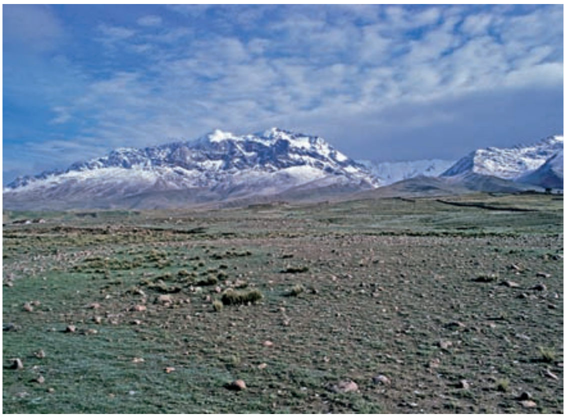


Fig. 8.18 Grazed puna, 4 km SW Santa Rosa, Puno, Peru, February 1975. Habitat of *Gastrotheca marsupiata*. Photo by W. E. Duellman.

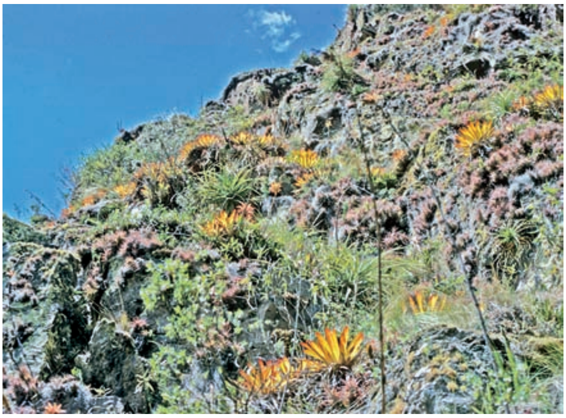


Fig. 8.19 Bromeliads on cliffs of the Cordillera Vilcanota, at Chilca, 2760 m, Cusco, Peru, January 1971. Habitat of *Gastrotheca ochoai*. Photo by W. E. Duellman.

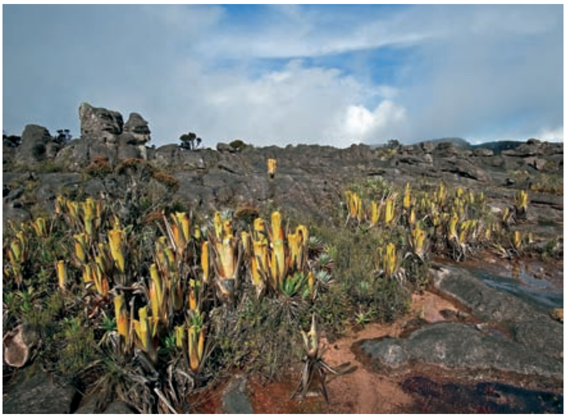


Fig. 8.20 Crest of Aprada-tepui, 2572 m, Bolívar, Venezuela, June 2012. *Stefania satelles* inhabits the terrestrial bromeliads. Photo with permission granted by the photographer, P. J. R. Kok.

1999). *Fritziana* and two subgenera of *Gastrotheca* are among these endemics. Most of this region is subjected to heavy cloud cover in the lowlands in the morning and in the mountains later in the day. A diversity of bromeliads is abundant; they are found from the beaches of the Atlantic Ocean to high elevations in the mountains (Fig. 8.9). In some non-forested areas in the mountains, terrestrial bromeliads are the homes of other species of frogs (Fig. 8.10). Disjunct areas of bamboo forest in the coastal lowlands provide a unique habitat (Fig. 8.11).

The Andes present a variety of habitats. Generally there is a gradual change latitudinally in the high elevations (3000 m and higher). In the Andes north of the Huancabamba Depression and some high regions in northern Peru, the environments above treeline are known as páramo; in many places they are conspicuous by the presence of cushion plants or the broad-leafed *Espeletia* (Asteraceae; Fig. 8.12). Tadpole-producing *Gastrotheca* utilize marshes and gullies in páramos for deposition of their tadpoles (Fig. 8.13). Some subpáramos have elfin forest and, in certain places, many terrestrial bromeliads (Fig. 8.14).

To the south of the Huancabamba Depression, the treeless areas are called puna. Especially in northern Peru, and along the crest of the Cordillera Oriental in that country, there are areas of humid puna containing a common bunchgrass (*Stipa*) and mosses (Fig. 8.15). In other places moisture condensation in clouds results in a fog-shrouded puna that may contain many mosses and lichens (Fig. 8.16). Most of the puna in central and southern Peru and in Bolivia is drier, and it is dominated by bunchgrasses of the genus *Stipa* (Fig. 8.17). Many areas in the Titicaca Basin are heavily grazed by sheep and/or llamas, but frogs do subsist there (Fig. 8.18). Bromeliads are abundant on Andean slopes; in some places they cling to cliffs bordering narrow valleys (Fig. 8.19). Bromeliads also are an important habitat on the tops of tepuis in the Guiana Highlands (Fig. 8.20).

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9

Genera of Hemiphractidae

FAMILY HEMIPHRACTIDAE

Hemiphractidae Peters, 1862:146.
Hemiphractinae Gadow, 1901:139, 210.
Amphignathodontinae Gadow, 1901:139, 188.
Opisthodelphyidae Lutz, 1968:18.
Leptodactylidae (in part) Faivovich et al., 2005:50.
Amphignathodontidae Frost et al., 2006:297.
Cryptobatrachidae Frost et al., 2006:297.
Hemiphractidae Frost et al., 2006:297.
Hemiphractidae Wiens et al., 2007:1887.

Definition

In hemiphractid frogs the pectoral girdle exhibits the arciferal condition (left and right halves overlapping ventrally, without articulation). A full complement of fingers (4) and toes (5) is present. The terminal phalange on each digit is claw-shaped and offset from the next-most distal phalange by a cartilaginous intercalary element. Amplexus and mating take place out of water. Fertilized eggs develop on the back of the female or in a pouch in the back of the female. The eggs undergo direct development or hatch as tadpoles in various stages; feeding tadpoles complete their development in ponds, whereas tadpoles that hatch at advanced stages and do not feed complete their development in phytotelma, such as bromeliads, tree holes, or bamboo. Embryos have one or two pairs of large sheet-like gills, with one or two gill stalks derived from Branchial Arches I and II. The habit of brooding eggs on the back or in a pouch and having large sheet-like gills are unique synapomorphies of hemiphractid frogs.

Distribution

The family occurs in humid tropical and subtropical forests in Costa Rica, Panama, and Venezuela (including the islands of Tobago and Trinidad), as well as in páramo and puna above treeline in Colombia, Ecuador, Peru, Bolivia, and northwestern Argentina. It also is present in the Atlantic Coastal Forest in eastern and southeastern Brazil. It is absent in most of the Amazon Basin.

Content

Six genera, with 104 recognized species.

Etymology

The familial name is derived from the Greek inseparable prefix *hemisys*-, meaning "half," and the Greek *phraktos*, meaning "fenced in" or "protected." Wagler (1828) apparently applied the name in allusion to the transverse crest seemingly fencing in the head posteriorly.

Remarks

Throughout most of the twentieth century, all of the hemiphractid genera were placed in Hylidae, the family of New World tree frogs. Some authors (e.g., Duellman, 2001) recognized hemiphractids as a subfamily of Hylidae. Early analyses of limited molecular data and small taxon samplings (e.g., Faivovich et al., 2005) had mixed results and did not solidify the relationships of hemiphractid frogs (chapter 2).

KEY TO GENERA OF HEMIPHRACTIDAE

1. Head triangular, casqued, with projecting paraoccipital processes, fleshy proboscis, fang-like teeth, prominent mandibular odontoids, and dorsally protruding neural spines of vertebrae..*Hemiphractus*
   Head rounded, lacking paraoccipital processes, fleshy proboscis, mandibular odontoids, and protruding neural spines of vertebrae; teeth bicuspid......................2

2. Females having enclosed dorsal brood pouch ....*Gastrotheca*
   Females lacking brood pouch, or, if present, having longitudinal fold of skin middorsally 3

3. Larger frogs (snout–vent lengths of adult females more than 40 mm); eggs brooded openly on dorsum of female 4
   Smaller frogs (snout–vent lengths of adult females less than 40 mm); eggs brooded in open basin or within cavity formed by lateral folds that overlap medially.....5

4. Adhesive pads present on penultimate subarticular tubercles on fingers; dentigerous processes of vomers transverse at the level of neopalatines; single pair of small embryonic gills ....*Cryptobatrachus*
   Adhesive pads lacking on penultimate subarticular tubercles on fingers; dentigerous processes of vomers inclined well anterior to level of neopalatines; two pairs of large embryonic gills ....*Stefania*

5. Nasals small, widely separated medially; lateral folds of skin adhere middorsally to cover eggs; embryos have single pair of gills derived from Branchial Arch I ....*Flectonotus*
   Nasals large, nearly abutting medially; lateral folds of skin do not cover eggs; embryos have two pairs of gills derived from Branchial Arches I and II...............*Fritziana*

Cryptobatrachus Ruthven

Cryptobatrachus Ruthven, 1916:1.—Type species: *Cryptobatrachus boulengeri* Ruthven, 1916, by original designation.

Definition

The skull is well ossified, but the dermal roofing bones are no more than weakly exostosed and are not co-ossified with the overlying skin; the skull is bluntly rounded anteriorly and posterolaterally. The frontoparietals articulate medially throughout their lengths. The nasals are moderate to large and articulate medially or not. The neopalatines are edentate and not serrated. A ventral spur of the neopalatine articulates with the dentigerous process of the vomer, which lies in the plane of the neopalatines (Fig. 4.1); this is a feature unique to the genus. The maxillary, premaxillary, and vomerine teeth are bicuspid. The mandible lacks serrations and odontoids. The procoelous presacral vertebrae lack elongate neural spines. Adhesive discs are present on the penultimate subarticular tubercles on the fingers; this is another feature unique to the genus. Vocal slits and a vocal sac are absent. The submentalis muscle is moderate in size and araphic; the intermandibularis muscle is differentiated by the presence of an apical element and bears a median raphe, but lacks an aponeurosis posteriorly. A fleshy proboscis on the tip of the snout and fleshy tubercles on the upper eyelids are absent. The first finger is longer than the second; nuptial excrescences are present. The snout–vent length varies from 27 to 52 mm in males and from 48 to 75 mm in females. The eggs undergo direct development on the back of the female. There is a single pair of small external sheet-like gills that do not completely cover the embryo; one pair of gill stalks is derived from Branchial Arch I.

Distribution and Ecology

Frogs of the genus *Cryptobatrachus* inhabit humid forested slopes of the three Andean cordilleras north of about 4°50′ N in Colombia, the Sierra Nevada de

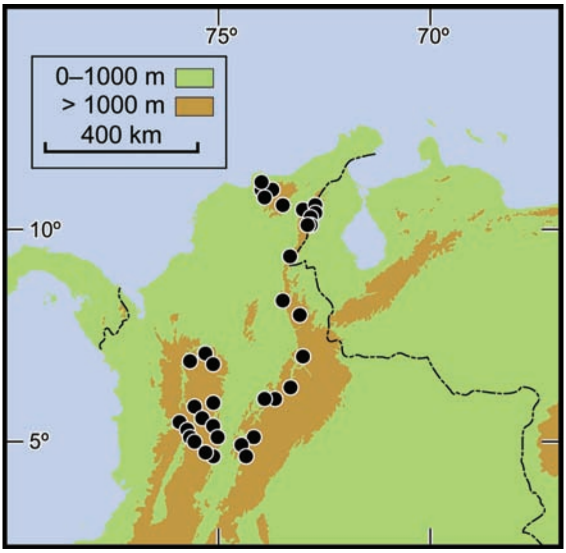

Fig. 9.1 Northwestern South America, showing the localities of known occurrences of *Cryptobatrachus*. Species are not designated.

Santa Marta in Colombia, and the Serranía de Perijá on the border of Colombia and Venezuela (Fig. 9.1). According to Lynch (2008) and Infante-Rivero et al. (2009), *Cryptobatrachus* has an elevational range of 360–2400 m. The frogs are nocturnal. They perch on limbs of low bushes and cling to rocks and cliffs in spray zones of waterfalls.

Content

Six species (Fig. 9.2): *Cryptobatrachus boulengeri* Ruthven, 1916; *C. conditus* Lynch, 2008; *C. fuhrmanni* (Peracca, 1914); *C. pedroruizi* Lynch, 2008; *C. remotus* Infante-Rivero, Rojas-Runjaic, and Barrio-Amorós, 2009; and *C. ruthveni* Lynch, 2008.

Etymology

The generic name is derived from the Greek *kryptos*, meaning “secret” or “hidden,” and the Greek *batrachos*, meaning “frog.” The name refers to the secretive habits of these frogs.

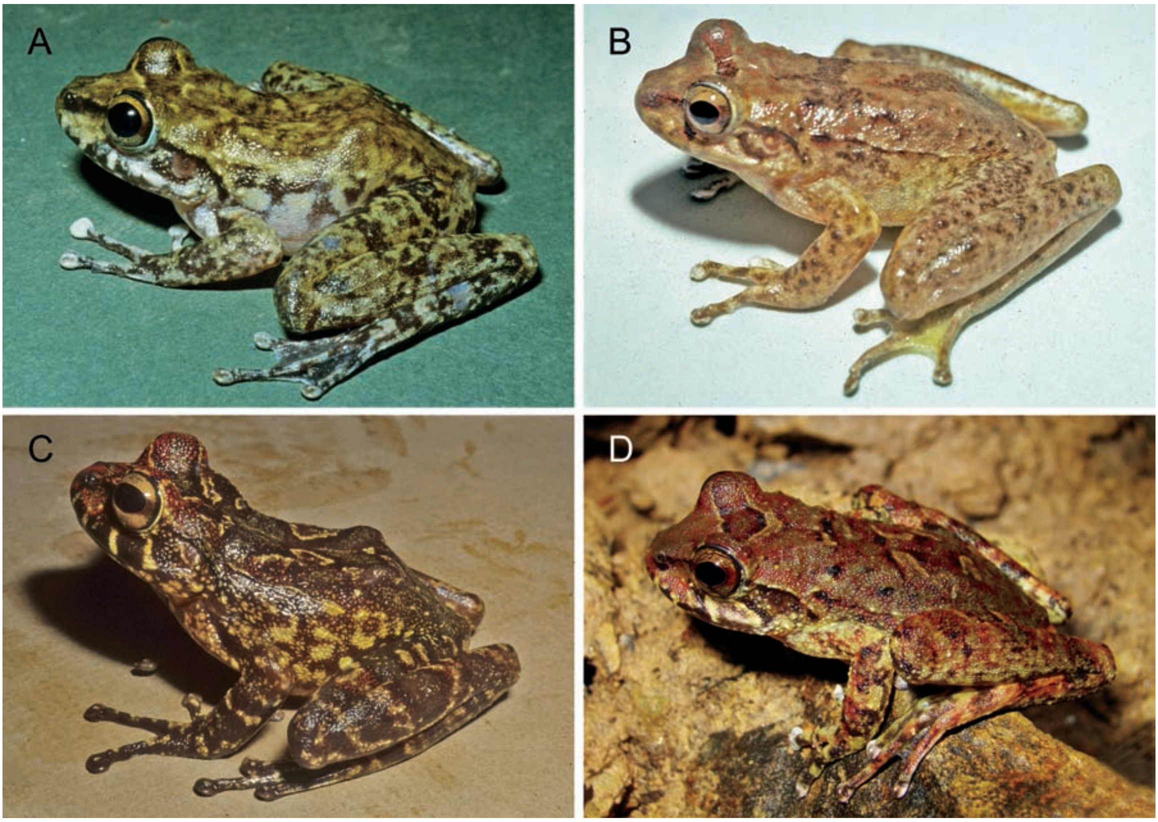

Fig. 9.2 Four species of *Cryptobatrachus*. A: *C. boulengeri*, from the Sierra Nevada de Santa Marta, Magdalena, Colombia. B: *C. conditus*, from 32 km W Sardinata, Norte de Santander, Colombia. C: *C. fuhrmanni*, from Colombia. D: *C. remotus*, from the Serranía de Perijá, Zulia, Venezuela. Photos by J. D. Lynch (A and C), W. E. Duellman (B), and F. J. M. Rojas-Runjaic (D), KUDA.

Remarks

Molecular analyses have included only one sample of *Cryptobatrachus*. In the tree presented by Blackburn and Duellman (2013), this sample is the sister taxon to *Gastrotheca*. A distinctly different and more reasonable placement of *Cryptobatrachus* as the sister taxon to *Stefania* was in the phylogenetic tree presented by Schmid et al. (2013). Neither arrangement is well supported, and relationships within the genus are unknown.

The late Pedro M. Ruíz-C. had gathered data on *Cryptobatrachus* from throughout Colombia but left no manuscript. Lynch (2008) summarized Ruíz's data, defined *Cryptobatrachus*, and provided brief accounts of the species. He recognized *C. nicefori*, which was described by Cochran and Goin (1970), despite the fact that the only known specimen lacks features characteristic of *Cryptobatrachus* (e.g., adhesive discs on the penultimate subarticular tubercles on the fingers, dorsolateral folds, and expanded terminal digits). Amézquita (2004) and Infante-Rivero et al. (2009) recognized the differences of *C. nicefori* from other members of the genus and suggested that *C. nicefori* actually was a member of the *Hyla bogotensis* group [= *Hyloscirtus*, as recognized by Faivovich et al., 2005].

Flectonotus Miranda-Ribeiro

Flectonotus Miranda-Ribeiro, 1926:109.—Type species: *Nototrema pygmaeum* Boettger, 1893, by original designation.

Definition

The skull is well ossified, but the dermal roofing bones are neither exostosed nor co-ossified with the overlying skin. The frontoparietals articulate medially throughout their lengths. The nasals are small and do not articulate medially. The neopalatines are edentate and not serrated. The maxillary, premaxillary, and vomerine teeth are bicuspid. The mandible lacks serrations and odontoids. The procoelous presacral vertebrae lack elongate neural spines. Adhesive discs are absent on the penultimate subarticular tubercles on the fingers. Vocal slits and a vocal sac are absent. The submentalis muscle is moderate in size and araphic; the intermandibularis muscle is undifferentiated, has a median raphe, and has a small aponeurosis posteriorly. A fleshy proboscis on the tip of the snout and fleshy tubercles on the upper eyelids are absent. The first finger is shorter than the second; nuptial excrescences are present. The snout–vent length varies from 16 to 26 mm in males and from 19 to 32 mm in females. The eggs develop into non-feeding tadpoles in a pouch with a longitudinal opening on the back of the female. The single pair of gills, which only cover about half of the developing embryo, are derived from Branchial Arch I; the gills and their stalks are separate.

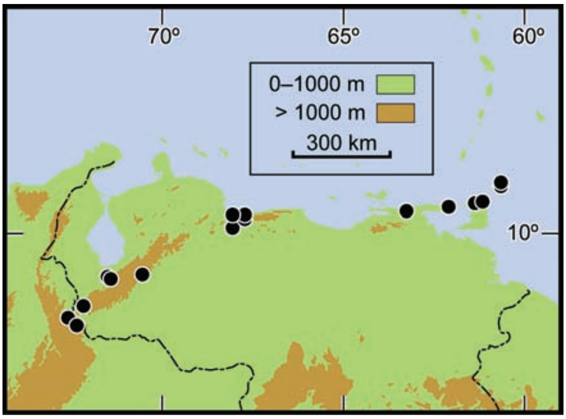

Fig. 9.3 Northern South America and Trinidad and Tobago, showing the localities of known occurrences of *Flectonotus*. Species are not designated.

Females of the genus *Flectonotus* differ from other hemiphractid frogs, except *Fritziana*, in that the brood pouch develops as a pair of lateral folds that grow over the eggs developing on the back of the female. Thus they differ from *Cryptobatrachus*, *Hemiphractus*, and *Stefania*, in which the eggs develop openly on the back of the female, and from *Gastrotheca*, in which the pouch develops as an invagination on the back of the female.

Distribution and Ecology

The genus has a discontinuous distribution in the Cordillera Oriental in northeastern Colombia, the adjacent Andes in western Venezuela, the Cordillera de la Costa and Península de Paria in northern Venezuela, and the islands of Trinidad and Tobago (Fig. 9.3). On the island of Trinidad, *Flectonotus fitzgeraldi* is found in leaf litter by day and on low vegetation at night. *Fl. pygmaeus* inhabits bromeliads.

Content

Two species (Fig. 9.4): *Flectonotus fitzgeraldi* (Parker, 1933) and *Fl. pygmaeus* (Boettger, 1893).

Etymology

The generic name is derived from the Latin *flecto*, meaning "bend," and the Greek *notos*, meaning "back."

Remarks

Among the species presently placed in this genus, Duellman and Gray (1983) recognized *Flectonotus* with

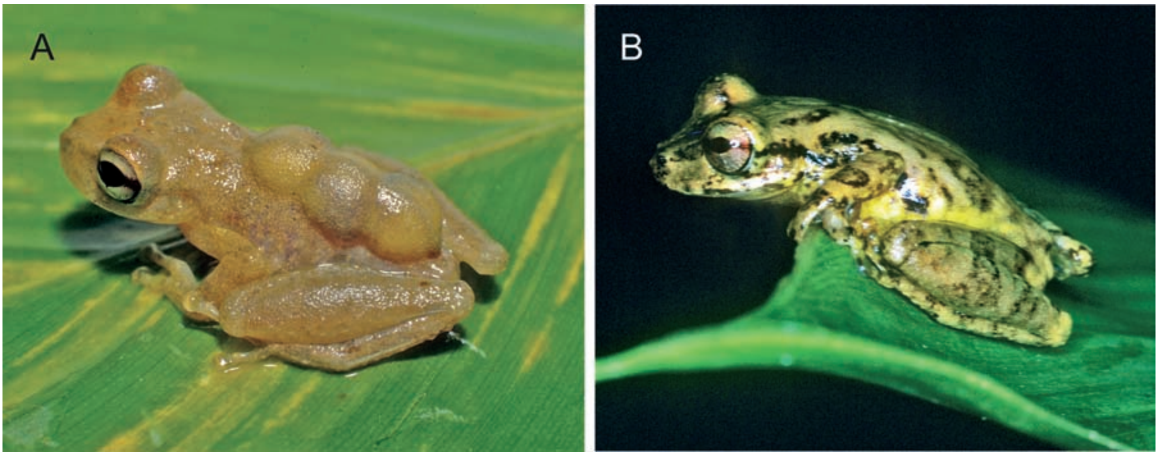

Fig. 9.4 The two named species of *Flectonotus*. A: *F. fitzgeraldi*, from Trinidad. B: *F. pygmaeus*, from the Estación Biológica Rancho Grande, Aragua, Venezuela. Photos by C. W. Myers (A) and W. E. Duellman (B), KUDA.

two species in Venezuela, Tobago, and Trinidad and *Fritziana* with three species in southeastern Brazil. Additional reproductive data and a reinterpretation of the morphological data by Weygoldt and Carvalho-e-Silva (1991) resulted in their placing *Fritziana* in the synonymy of *Flectonotus*. Duellman et al. (2011) later showed that developmental, morphological, and molecular differences distinguish the two genera; furthermore, these authors' molecular analysis revealed that *Flectonotus* and *Fritziana* are not one another's closest relatives. The Venezuelan and insular *Flectonotus* are characterized by the following: (1) lateral folds of skin of the brood pouch adhere medially over the eggs; (2) embryos have a single pair of external gills, each with a single stalk; (3) obligatory non-feeding larvae have weakly cornified beaks and lack denticles and papillae; and (4) nasal bones in adults are broadly separated medially. *Fritziana* in southeastern Brazil are characterized as follows: (1) lateral folds of skin form a shallow basin in which the eggs develop (folds extend dorsally in *Fr. fissilis*); (2) embryos have two pairs of gills, each with a single stalk; (3) facultative non-feeding larvae have keratinized beaks and small papillae but lack denticles; and (4) nasal bones in adults are large and nearly in contact medially. Other differences between Venezuelan and Brazilian taxa exist in their chromosome numbers (Schmid et al., 2013).

The phylogenetic arrangement resulting from molecular analyses places *Cryptobatrachus* and *Flectonotus* as sister-groups that are the basal hemiphractids. This arrangement is supported by the embryos having only a single gill stalk and a single pair of relatively small sheet-like external gills. This is in contrast to two pairs of larger gills in other hemiphractids.

Hemiphractus Wagler

Hemiphractus Wagler, 1828:743.—Type species: *Hemiphractus spixii* Wagler, 1828 [= *Rana scutata* Spix, 1824] by monotypy.

Cerathyla Jiménez de la Espada, 1871:63.—Type species: *Cerathyla bubalus* Jiménez de la Espada, 1871, by subsequent designation (G. Myers and Carvalho, 1945:21). Synonymy fide Noble: 1926:19.

Definition

The skull is extensively casqued and characterized by prominent posterolaterally projecting paraoccipital processes (Fig. 4.2). The dermal roofing bones are exostosed in a reticulate and/or tuberculate pattern of dermal sculpturing, but they are not co-ossified with the overlying skin. The neopalatines are edentate but serrated. The maxillary, premaxillary, and vomerine teeth are fang-like and curved inward. The mandible bears odontoid serrations and a pair of enlarged fang-like odontoids near the mandibular symphysis. The arciferal pectoral girdle has small clavicles, massive coracoids, and broadly overlapping epicoracoid cartilages. The procoelous presacral vertebrae have enlarged neural spines that protrude dorsally. Vocal slits and a vocal sac are absent. The submentalis muscle is extremely small and araphic; the intermandibularis muscle is undifferentiated, incompletely developed anteriorly, and bears an extensive median aponeurosis. There is a small fleshy proboscis on the tip of the snout and one or more fleshy tubercles on each upper eyelid. The first finger is longer than the second; nuptial excrescenses are absent. The snout–vent length varies from 38 to 57 mm in males and from 40 to 81 mm in females. The eggs develop into froglets on the back of the female. The gills, which entirely cover the developing embryo, are derived from Branchial Arches I and II; the gills and their stalks are separate (fused in *Hemiphractus fasciatus*).

No other hemiphractids have a fleshy proboscis, projecting paraoccipital processes, fang-like teeth, prominent mandibular odontoids, and dorsally protruding neural spines of the vertebrae. In fact, *Hemiphractus* cannot be confused with any other New World frog. A frog that is similar in appearance is *Ceratobatrachus guentheri* Boulenger, a member of Ceratobatrachidae (Frost et al., 2006) endemic to the Solomon Islands. This terrestrial frog differs from *Hemiphractus* by having a firmisternal pectoral girdle and lacking dorsally protruding neural spines on the presacral vertebrae, enlarged mandibular odontoids, and intercalary cartilages in the hands and feet. The eggs are deposited on the ground, where they undergo direct development (Pikacha et al., 2008).

Distribution and Ecology

The genus has a disjunct distribution in humid tropical forests. It ranges from western Panama to the Pacific slopes of Colombia and northwestern Ecuador and then occurs on the forested slopes of the Andes and upper Amazon Basin in Colombia, Ecuador, extreme western Brazil, and northern Bolivia (Fig. 9.5). *Hemiphractus scutatus* inhabits the forest floor, whereas the other species are arboreal, inasmuch as they usually are observed on leaves or branches of low trees and bushes at night. These frogs are voracious carnivores and eat large insects (e.g., orthopterans), other frogs, and small lizards (Trueb, 1974).

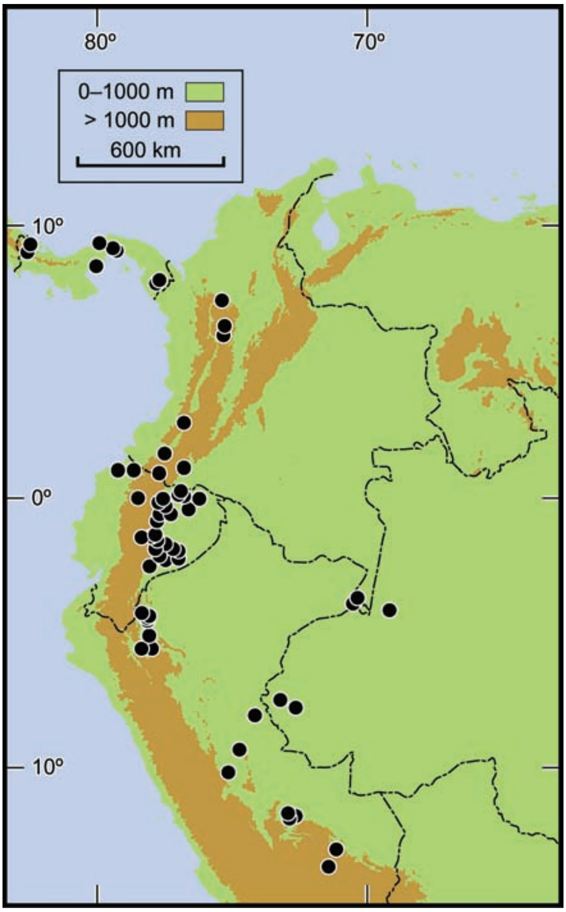

Fig. 9.5 Northwestern South America, showing the localities of known occurrences of *Hemiphractus*. Species are not designated.

Content

Six species (Fig. 9.6): *Hemiphractus bubalus* (Jiménez de la Espada, 1871); *H. fasciatus* Peters, 1862; *H. helioi* Sheil and Mendelson, 2001; *H. johnsoni* (Noble, 1917); *H. proboscideus* (Jiménez de la Espada, 1871); and *H. scutatus* (Spix, 1824).

Etymology

The generic name, like the familial name, is derived from the Greek inseparable prefix *hemisys*-, meaning "half," and the Greek *phraktos*, meaning "fenced in" or "protected." Wagler (1828) apparently applied the name in allusion to the transverse crest seemingly "fencing in" the head posteriorly.

Remarks

Several authors (e.g., Sheil et al., 2001) have stated that the skin on the head is co-ossified with the underlying cranial elements; this is not true. Although the pattern of sculpturing on the bones is visible externally, the skin is not co-ossified with the underlying bones; a fine probe can be easily moved laterally beneath the skin. Trueb (1974) reviewed the genus and considered *Hemiphractus johnsoni* to range from Colombia to Peru. Sheil and Mendelson (2001) subsequently redescribed *H. johnsoni* and assigned specimens formerly referred to *H. johnsoni* from Ecuador and Peru to a new species, *H. helioi*. As noted by Wiens et al. (2007), the suggestion that *Hemiphractus* is nested within *Gastrotheca* (Mendelson et al., 2000) may have been caused by misleading phylogenetic signals associated with hyperossification of the skull. A phylogenetic analysis based on morphological characters by Sheil et al. (2001) revealed a topology that is somewhat like the analysis herein, based on molecular data.

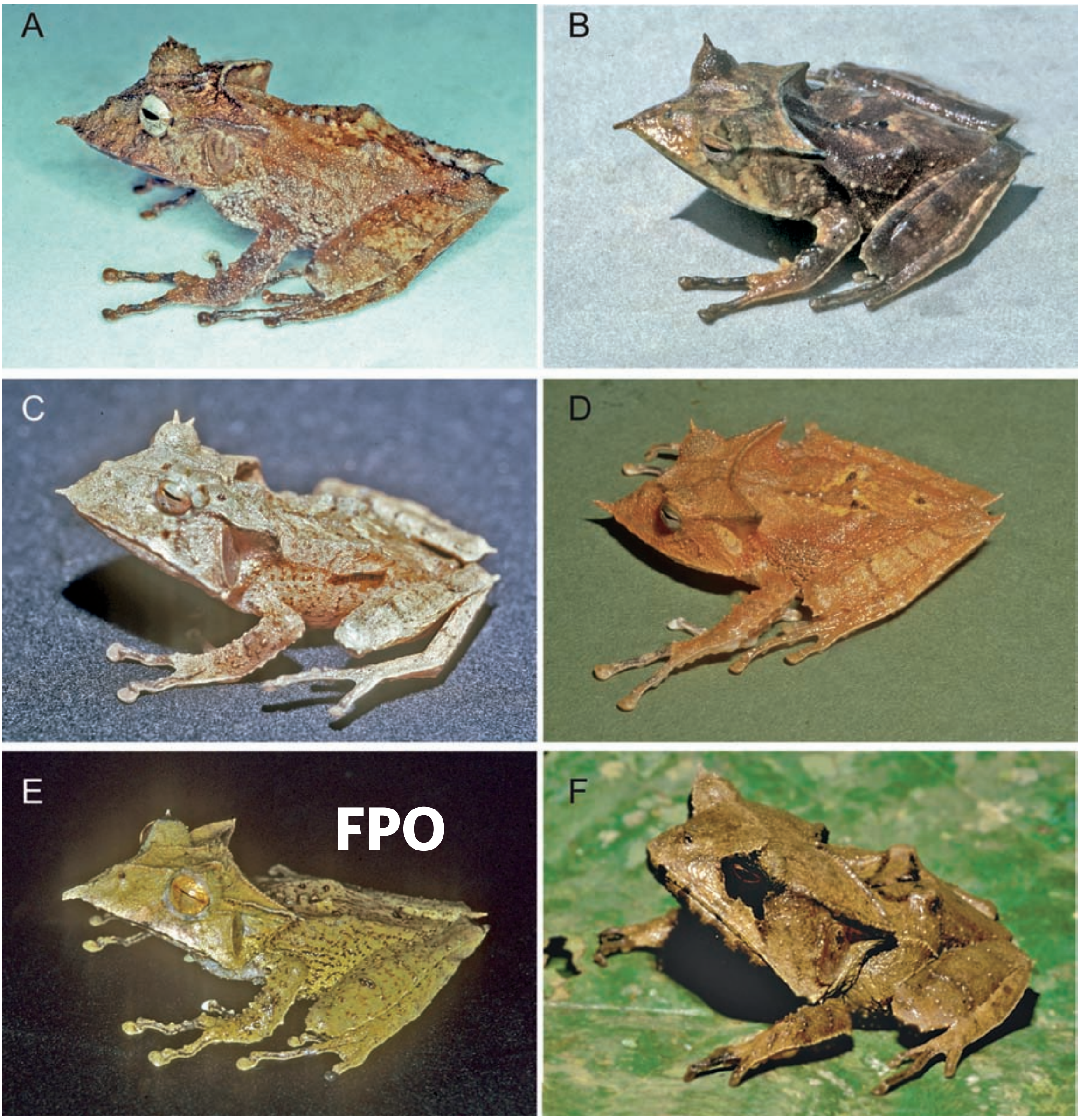

Fig. 9.6 The species of *Hemiphractus*. A: *H. bubalus*, from 10.3 km W El Pepino, 1440 m, Putumayo, Colombia. B: *H. fasciatus*, from SE slope Cerro Pirre, 1100 m, Darién, Panama. C: *H. helioi*, from Río Kosñipata, 4 km SW Santa Isabela, 1700 m, Cusco, Peru. D: *H. johnsoni*, from 1890 m, Departamento Caldas, Colombia. E: *H. proboscideus*, from Santa Cecilia, 340 m, Sucumbíos, Ecuador. F: *H. scutatus*, from Río Yarapa, Loreto, Peru. Photos by W. E. Duellman (A, C, and E), C. W. Myers (B), P. M. Ruíz-C. (D), and W. W. Lamar (F), KUDA.

Fritziana Mello-Leitão

Fritzia Miranda-Ribeiro, 1920:321.—Type species: *Hyla goeldii* Boulenger, 1895, by original designation. Preoccupied by *Fritzia* Cambridge [Arachnida].

Coelonotus Miranda-Ribeiro, 1920:327.—Type species: *Coelonotus fissilis* Miranda-Ribeiro, 1920, by original designation. Preoccupied by *Coelonotus* Peters [Pisces].

Fritziana Mello-Leitão, 1937:330. New name for *Fritzia* Miranda-Ribeiro, 1920.

Nototheca Bokermann, 1950:217. New name for *Coelonotus* Miranda-Ribeiro, 1920.

Flectonotus (in part)—Weygoldt and Carvalho-e-Silva, 1991:78.

Definition

The skull is well ossified, but the dermal roofing bones are neither exostosed nor co-ossified with the overlying skin. The frontoparietals articulate medially throughout their lengths. The nasals are large and nearly in contact anterior to the sphenethmoid. The neopalatines are edentate and not serrated. The maxillary, premaxillary, and vomerine teeth are bicuspid. The mandible lacks serrations and odontoids. The procoelous presacral vertebrae lack elongate neural spines. Adhesive discs are absent on the penultimate subarticular tubercles on the fingers. Vocal slits and a vocal sac are present. The submentalis muscle is moderate in size and araphic; the intermandibularis muscle is undifferentiated, has a median raphe, and has a small aponeurosis posteriorly. A fleshy proboscis on the tip of the snout and fleshy tubercles on the upper eyelids are absent. The first finger is shorter than the second; nuptial excrescences are present. The snout–vent length varies from 18 to 34 mm in males and from 25 to 39 mm in females. The eggs develop into non-feeding tadpoles in a basin between lateral folds of skin on the back of the female. Two pairs of gills, which only cover about half of the developing embryo, are derived from Branchial Arches I and II; the gills and their stalks are separate.

Females of the genus *Fritziana* differ from other hemiphractid frogs, except *Flectonotus*, in that the brood pouch develops as a pair of lateral folds, but these folds do not grow over the eggs developing on the back of the female and adhere to one another, as they do in *Flectonotus*. Thus these genera differ from *Cryptobatrachus*, *Hemiphractus*, and *Stefania*, in which the eggs develop openly on the back of the female, and from *Gastrotheca*, in which the pouch develops as an invagination on the back of the female.

Distribution and Ecology

The genus is distributed on the lowlands and on slopes of the coastal mountains to elevations of 2200 m in southeastern Brazil (Fig. 9.7). These frogs primarily inhabit arboreal and terrestrial bromeliads, as well as holes in bamboo.

Content

Four species (Fig. 9.8): *Fritziana fissilis* (Miranda-Ribeiro, 1920), *Fr. goeldii* (Boulenger, 1895), *Fr. ohausi* (Wandolleck, 1907), and *Fr. ulei* (Miranda-Ribeiro, 1926).

Etymology

The generic name is a new name proposed for *Fritzia*, which is an arachnid.

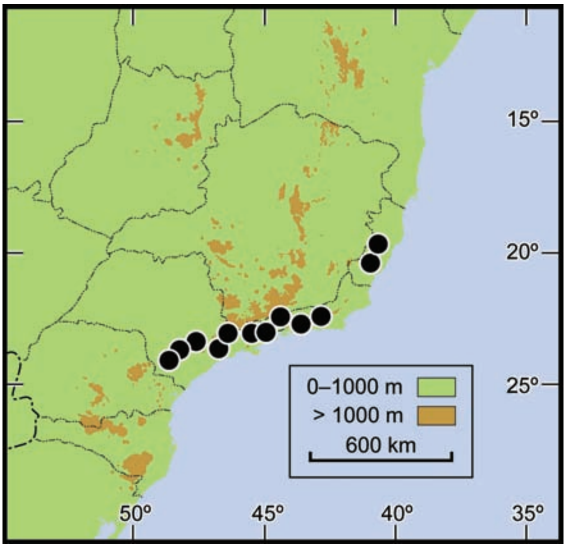

Fig. 9.7 Southeastern Brazil, showing the localities of known occurrences of *Fritziana*. Species are not designated.

Remarks

See "Remarks" in the account of *Flectonotus*. The recent recognition of *Fritziana ulei* was by Folly et al. (2014). Apparently there is at least one undescribed species in southeastern Brazil.

Stefania Rivero

Stefania Rivero, 1968:142.—Type species: *Hyla evansi* Boulenger, 1904, by original designation.

Definition

The skull is well ossified, but the dermal roofing bones are neither exostosed nor co-ossified with the overlying skin. Some species have cranial crests resulting from elevated lateral edges of the frontoparietals, which articulate medially throughout their lengths. The nasals are large and in contact anterior to the sphenethmoid. The neopalatines are edentate and not serrated. A ventral spur of the neopalatine is absent. The dentigerous processes of the vomers are anterior to the neopalatines. The maxillary, premaxillary, and vomerine teeth are bicuspid. The mandible lacks serrations and odontoids. The procoelous presacral vertebrae lack elongate neural spines. Adhesive discs are absent on the penultimate subarticular tubercles on the fingers. Vocal slits and a vocal sac are absent. The submentalis muscle is moderate in size and araphic; the intermandibularis muscle is a single sheet or is differentiated by the presence of an

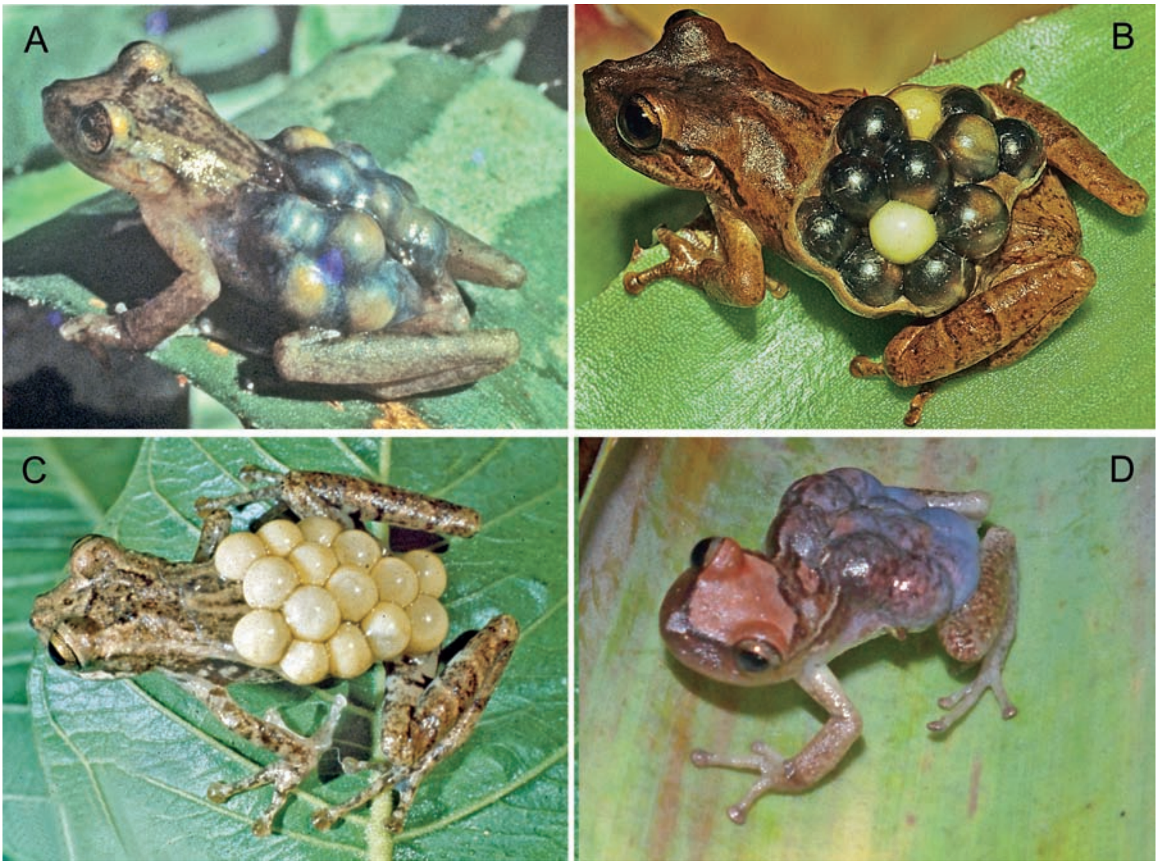

Fig. 9.8 The four species of *Fritziana* in southeastern Brazil. A: *F. fissilis*, from Serra da Bocaina, São Paulo. B: *F. goeldii*, from Rio de Janeiro, Rio de Janeiro. C: *F. ohausi*, from Casa Grande, São Paulo. D: *F. ulei*, from Lumiar, Nova Friburgo, 1316 m, Rio de Janeiro. Photos by W. C. A. Bokermann (A and C), K.-H. Jungfer (B), and C. de Luna-Dias Neto (D), KUDA.

apical element and bears a median raphe, but lacks an aponeurosis posteriorly. A fleshy proboscis on the tip of the snout and fleshy tubercles on the upper eyelids are absent. The first finger is longer than the second; nuptial excrescences are present. Males are notably smaller than females, some of which reach nearly 100 mm in their snout–vent length. The eggs develop into froglets on the back of the female. The gills, which entirely cover the developing embryo, are derived from Branchial Arches I and II; the gills and their stalks are separate.

Distribution

Members of this genus occur in the Guianan Region of Guyana, southeastern Venezuela, and extreme northern Amazonas, Brazil (Fig. 9.9). With the exception of *Stefania evansi*, which has a broad distribution in the lowlands and highlands, the species of *Stefania* have disjunct distributions at elevations of 600–2450 m on the slopes and tops of table mountains (tepuis).

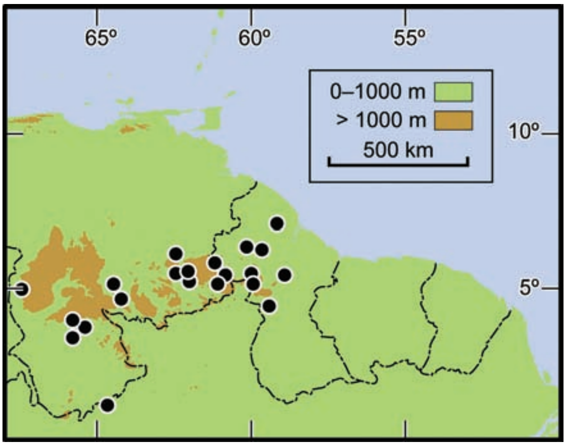

Fig. 9.9 Northeastern South America, showing the localities of known occurrences of *Stefania*. Species are not designated.

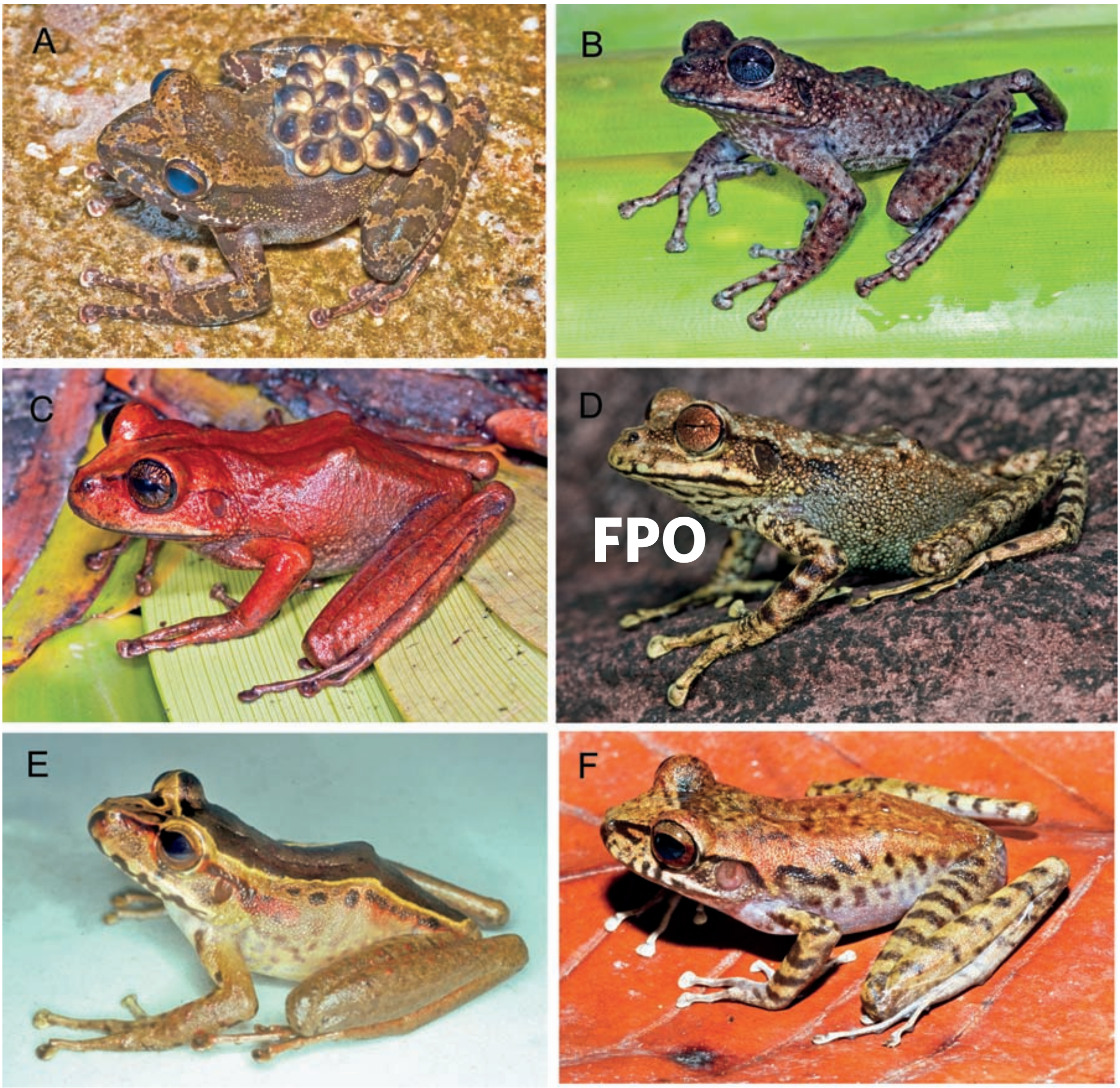

Fig. 9.10 Selected species of *Stefania*. A: *S. evansi*, female, 97.5 mm SVL, from Kaieteur National Park, Guyana. B: *S. ginesi*, female, 60.2 mm SVL, from Abakapa-tepui, Venezuela. C: *S. riveroi*, female, 48.2 mm SVL, from Yuruani-tepui, Venezuela. D: *S. satelles*, female, 52.2 mm SVL, from Aprada-tepui, Venezuela. E: *S. scalae*, male, 57.5 mm SVL, from Km 112, El Dorado–Santa Elena de Uiarén road, Venezuela. F: *S. woodleyi*, male, 47.1 mm SVL, from Kaieteur National Park, Guyana. Photos A–D and F with permission granted by the photographer, P. J. R. Kok; E by W. E. Duellman.

Content

Nineteen species (Fig. 9.10): *Stefania ackawaio* MacCulloch and Lathrop, 2002; *S. ayangannae* MacCulloch and Lathrop, 2002; *S. breweri* Barrio-Amorós and Fuentes, 2003; *S. coxi* MacCulloch and Lathrop, 2002; *S. evansi* (Boulenger, 1904); *S. ginesi* Rivero, 1968; *S. goini* Rivero, 1968; *S. marahuaquensis* (Rivero, 1961); *S. oculosa* Señaris, Ayarzagüena, and Gorzula, 1997; *S. neblinae* Carvalho, MacCulloch, Bonora, and Vogt, 2010; *S. percristata* Señaris, Ayarzagüena, and Gorzula, 1997; *S. riae* Duellman and Hoogmoed, 1984; *S. riveroi* Señaris, Ayarzagüena, and Gorzula, 1997; *S. roraimae* Duellman and Hoogmoed, 1984; *S. satelles* Señaris, Ayarzagüena, and Gorzula, 1997; *S. scalae* Rivero, 1970; *S. schuberti* Señaris, Ayarzagüena, and Gorzula, 1997; *S. tamacuarina* Myers and Donnelly, 1997; and *S. woodleyi* Rivero, 1968.

Etymology

The generic name *Stefania* is a patronym for Luis Stefani.

Remarks

Duellman and Hoogmoed (1984) considered *Cryptobatrachus* to be the sister-group to *Stefania* for the species in which they provided a phylogenetic analysis based on morphology. Another hypothesized phylogeny based on morphology and reproductive features by Mendelson et al. (2000) included only one species of *Stefania*, which was clustered with *Gastrotheca* and not with *Cryptobatrachus*. Only five species were included in a phylogenetic reconstruction based on molecular data by Wiens et al. (2007); the five species formed a clade that is the sister-group to *Hemiphractus*. The analysis by Blackburn and Duellman (2013) and the one presented here (chapter 3) show *Stefania* to be the sister-group to *Gastrotheca*. The last comprehensive review of these frogs was by Señaris et al. (1997); nearly a third of the recognized species have been described since then. No modern phylogenetic analysis of *Stefania* is available; the genus is under scrutiny by P. Kok. Salerno and Pauly (2012) reported on sizes and numbers of eggs brooded by 46 individuals of eight species. The largest number of eggs transported by a female is 30, on an *S. evansi*.

Gastrotheca Fitzinger

Gastrotheca Fitzinger, 1843.—Type species: *Hyla marsupiata* Duméril and Bibron, 1841, by monotypy.

Notodelphys Lichtenstein and Weinland, 1854:373.—Type species: *Notodelphys ovifera* Lichtenstein and Weinland, 1854, by monotypy. Preoccupied by *Notodelphys* Allman, 1847 [Crustacea].

Nototrema Günther, 1859:115. Substitute name for *Gastrotheca* Fitzinger, 1843.

Opisthodelphys Günther, 1859:117. New name for *Notodelphys* Lichtenstein and Weinland, 1854.

Amphignathodon Boulenger, 1882.—Type species: *Amphignathodon guentheri* Boulenger, 1882, by monotypy.

Duellmania Dubois, 1987:32.—Type species: *Hyla argenteovirens* Boettger, 1892, by original designation.

Definition

The skull is well ossified, but the dermal roofing bones are exostosed and are co-ossified with the overlying skin in some species. The frontoparietals articulate medially throughout their lengths in most species. The nasals are large and in contact anterior to the sphenethmoid. The neopalatines are edentate and serrated or not. A ventral spur of the neopalatine is absent. The dentigerous processes of the vomers are anterior to the neopalatines. The maxillary, premaxillary, and vomerine teeth are bicuspid. The mandible lacks serrations; odontoids are present in one species and true teeth are present on the dentary in one species. The procoelous presacral vertebrae lack elongate neural spines. Adhesive discs are absent on the penultimate subarticular tubercles on the fingers. Vocal slits and a vocal sac usually are present. The submentalis muscle is moderate in size and araphic; the intermandibularis muscle is a single sheet or is differentiated by the presence of an apical element and bears a median raphe, but lacks an aponeurosis posteriorly. A fleshy proboscis on the tip of the snout and fleshy tubercles on the upper eyelids are absent. The first finger is longer or shorter than the second; nuptial excrescences usually are present. The snout–vent length varies from 26 to 86 mm in males and from 32 to 110 in females. The eggs undergo direct development or hatch as free-swimming feeding tadpoles in a pouch on the back of the female. The embryonic gills, which entirely cover the developing embryo, are derived from Branchial Arches I and II; the gill stalks remain separate, but the gills fuse to form a bell-shaped structure.

Distribution

This genus has a broad distribution from the Caribbean versant in Costa Rica and Panama and the Pacific versant from eastern Panama to Ecuador, as well as in the Andes from Venezuela and Colombia to central Argentina. It also occurs on the upper Amazon Basin in Ecuador and northern Peru, the Cordillera de la Costa in northern Venezuela, and the Atlantic Coastal Forest in eastern Brazil (Fig. 9.11). The greatest number of species is in the Andes of Colombia (16 species, 6 endemic), Ecuador (16 species, 5 endemic), and Peru (16 species, 11 endemic).

Content

Sixty-seven species, for which 77 names have been proposed (Table 3.2).

Etymology

The generic name is derived from the Greek *gastros*, meaning "belly," and the Greek *theke*, meaning "container"; presumably Fitzinger (1843) was referring to the brood pouch on the dorsum in females. Günther (1859:115) noted that Fitzinger (1843) had erred in his choice of a generic name and stated: "Fitzinger ap-

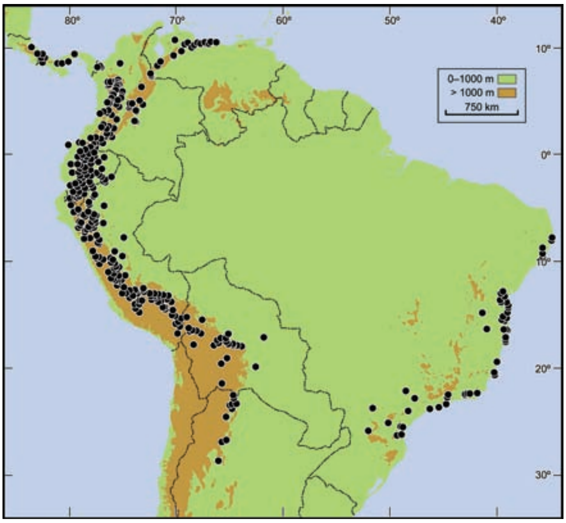

Fig. 9.11 South America and lower Central America, showing the localities of known occurrences of *Gastrotheca*; many localities are not shown because of overcrowding. Species are not designated.

pears to have believed in the existence of a pouch on the belly; his denomination . . . [was] used by the old anatomists for the brain-pan; therefore I think myself justified in not accepting his name." Günther therefore proposed the name *Nototrema* (from the Greek *notos*, meaning "back"), in reference to the position of the brood pouch. Even though Günther's substitute name is more appropriate, the Law of Priority necessitates the use of the misleading generic name *Gastrotheca*.

Remarks

Numerous generic names have been applied to the marsupial frogs, the first species of which was described as *Hyla marsupiata* by Duméril and Bibron (1841). In his wholesale recognition of new genera, Fitzinger (1843) proposed the generic name *Gastrotheca* for *H. marsupiata* Duméril and Bibron, 1841.

Günther (1859), in addition to proposing the substitute name *Nototrema*, also noted that *Notodelphys* Lichtenstein and Weinland, 1854, was preoccupied by Allman's name for a crustacean and instead proposed the substitute name *Opisthodelphys*. The latter name was seldom used. Boulenger (1882 et seq.) used *Nototrema* for all marsupial frogs, and that generic name remained in vogue through the 1940s, although Gaige (1922, 1933), Miranda-Ribeiro (1926), A. Lutz and Lutz (1939), and Dunn (1944) described new species as *Gastrotheca*.

Amphignathodon was recognized as a monotypic genus since the description of *A. guentheri* by Boulenger (1882), because of the possession of teeth on the dentary. The species was considered to be a member of the *Gastrotheca cornuta* group by Duellman et al. (1988).

Using data published by other workers, Dubois (1987) recognized numerous subgenera, many of which were new names. Within *Gastrotheca*, he placed all species having direct development in the subgenus *Opisthodelphys*, species having free-living tadpoles and a frontoparietal fontanelle in the subgenus *Gastrotheca*, and species having free-living tadpoles and lacking a frontoparietal fontanelle in the subgenus *Duellmania*.

Herein, as a matter of convenience, I recognize six subgenera; each contains a monophyletic group of *Gastrotheca*. These subgenera and the species included in each are treated in detail in chapters 10–12.

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10

Basal Subgenera of *Gastrotheca*

Herein are the accounts of the subgenera *Amphignathodon*, *Australotheca*, *Cryptotheca*, *Edaphotheca*, *Eotheca*, and *Opisthodelphys*, and the species included within them.

Subgenus *Eotheca*, new subgenus

Eotheca Duellman.—Type species: *Nototrema fissipes* Boulenger, 1888.

Definition

Members of the subgenus *Eotheca* are large and casque headed, with the skin co-ossified with the dermal roofing bones of the skull. The snout–vent lengths of most adults of both sexes are in excess of 70 mm. In females this length exceeds 80 mm; the largest known specimen of the subgenus is a female *Gastrotheca megacephala* having a snout–vent length of 110 mm. The mean percentage of tibia length to snout–vent length is less than 50%, except in *G. recava*, in which it is 52.3%. The head is large, and wider than long (head width 38.7%–41.2% of snout–vent length, and head length 35.2%–36.5% of snout–vent length), except in *G. recava*, in which the mean head width and head length are 35.7% and 39.6% of the snout–vent length, respectively. All species lack dermal ornamentation. The dorsum is tan or greenish tan, with or without brown markings.

This subgenus is supported by six osteological synapomorphies that, taken together, distinguish it from its sister taxa. Owing to the expansion of the head of the squamosal and the otic flange of the frontoparietal, the temporal arcade is complete over the otic region, which is not especially well ossified. The alary processes of the premaxillae are nearly vertical; thus in lateral profile the snout is high and truncate. All of these frogs have a massive postorbital process on the maxilla that bears a horizontal articulation with the wide (but short) zygomatic ramus of the squamosal. The otic plate of the squamosal is barely developed, and narrowly overlaps the cartilaginous lateral margin of the crista parotica. The neopalatines are moderately to narrowly separated from one another. The dentigerous processes of the vomers are located between the anterior quadrants of the choanae.

Reproduction

Females of all species in the subgenus *Eotheca* produce eggs that undergo direct development into froglets.

Distribution

This subgenus occurs in refuges of the Atlantic Coastal Forest at elevations from near sea level to 530 m from Pernambuco southward to northern Espírito Santo, Brazil. One species, *Gastrotheca prasina*, is known from an inland locality, at an elevation of 989 m in the state of Minas Gerais. These refuges are thought to correspond to climatically stable humid forest regions during Plio-Pleistocene climatic fluctuations (Carnaval et al., 2009).

Content

Six species.

Etymology

The name is derived from the Greek *eos*, meaning "early," and the Greek *theke*, meaning "container." The name refers to the basal position of this clade of *Gastrotheca*.

Remarks

In the phylogenetic arrangement proposed by Wiens et al. (2007), *Gastrotheca fissipes* is the sister taxon to all other *Gastrotheca*. This position has been substantiated by molecular data from three other species (*G. megacephala*, *prasina*, and *recava*). The phylogenetic analysis presented herein (chapter 3) shows that the six species composing this subgenus are closely related and form the basal clade in *Gastrotheca*. Within this clade, *G. flamma* and *G. pulchra* are loosely associated with the four larger casque-headed species (Fig. 10.1). Molecular data are not available for *G. flamma*; provisionally it is placed as the sister species to *G. pulchra*, because of two shared derived characters: calcars on the heel, and a tubercle on the outer edge of the upper eyelid.

KEY TO SPECIES OF *EOTHECA*

1. Heel bearing triangular calcar 2
   Heel lacking triangular calcar 3

2. Two tubercles on margin of upper eyelid; tympanic annulus granular; no enlarged tubercles ventrolateral to cloacal opening .... *G. flamma*
   One tubercle on margin of upper eyelid; tympanic annulus smooth; as many as six tubercles ventrolateral to cloacal opening .... *G. pulchra*

3. Brown suborbital bar present 4
   Brown suborbital bar absent; entire labial region dark brown .... *G. recava*

4. Dorsum tan, with or without brown markings 5
   Dorsum green, with or without faint tan markings .... *G. prasina*

5. Dark chevron-shaped marks on body; transverse occipital crest absent .... *G. fissipes*
   No chevron-shaped marks on body; transverse occipital crest present .... *G. megacephala*

Gastrotheca (*Eotheca*) *fissipes* (Boulenger)

Nototrema fissipes Boulenger, 1888:42.—Holotype: BMNH 1947.2.22.40 from "Iguarasse" [= Iguaraçu], Estado do Pernambuco, Brazil.
Gastrotheca fissipes—Gorham, 1963:21.
Gastrotheca (*Opisthodelphys*) *fissipes*—Dubois, 1987:31.

Diagnosis

Adults of this large species attain a snout–vent length of 70 mm in females and 68 mm in males. The tibia length is less than 55% of the snout–vent length, and is slightly longer than the foot. The interorbital distance is about twice the width of the upper eyelid. The skin on the dorsum is smooth to finely granular, co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is much longer than the second. The discs on the

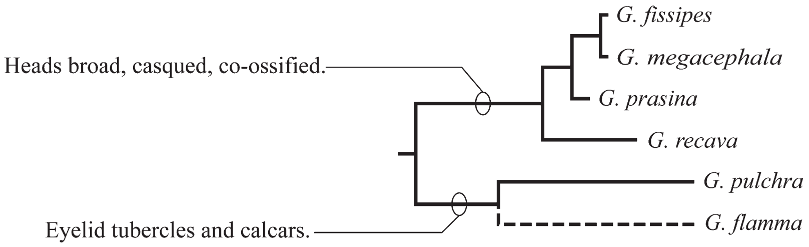
G. fissipes
G. megacephala
G. prasina
G. recava
G. pulchra
G. flamma
Heads broad, casqued, co-ossified.
Eyelid tubercles and calcars.

Fig. 10.1 Hypothesized phylogenetic relationships among species of the subgenus *Eotheca*, based on molecular data; the one species lacking molecular data is tentatively placed (dashed line), based on morphological synapomorphies.

fingers are slightly wider than the digits. The fingers are unwebbed; on the foot webbing is absent between the first, second, and third toes, and basal between the outer toes. The dorsum is tan, with narrow darker brown chevrons. Markings on the head consist of a dark brown interorbital bar, subocular bar, and broad postorbital stripe. A pale dorsolateral stripe is absent. The flanks are creamy tan; the venter is cream, with a brown suffusion on the chest.

Gastrotheca fissipes is most like the somewhat larger *G. megacephala*, and is also similar to *G. prasina*, all of which have extensively co-ossified skulls. Both of the latter species differ from *G. fissipes* by lacking chevron-shaped marks on the dorsum, and by having a different configuration of the posterior end of the skull. In all three species the bony supratympanic crest extends to the level of the posterior edge of the tympanum; in *G. fissipes* the posterior margin of the skull is scalloped, and lacks a transverse occipital crest, which is evident and continuous with the supratympanic crests in *G. megacephala* and *G. prasina*. *G. recava* differs from *G. fissipes* by lacking a broad brown labial bar below the orbit; instead, the entire labial and postorbital regions are dark brown, a color continuous onto the flanks. Furthermore, the configuration of the cranial roofing bones is distinctly different; the frontoparietals have a narrow articulation with the squamosal, in contrast to the broad articulation in *G. fissipes*. Also, in *G. fissipes* the dermal sphenethmoid is much smaller than that in *G. recava*; *G. fissipes* differs from the smaller *G. flamma* and *G. pulchra* by lacking calcars and tubercles on the eyelids.

Description

The following description is based on five adults. The body is robust; males attain a snout–vent length of 69.7 mm, and 81.5 mm in females. The head is much wider than long, and as wide as the body. The snout is narrowly truncate terminally, but acutely rounded in general shape, and is high and truncate in profile. The canthus rostralis is acutely angular in cross-section. The loreal region is concave; the lips are shallowly rounded, and nearly vertical. The top of the head is flat. The interorbital distance is at least twice the width of the upper eyelid. The internarial area is slightly depressed. The nostrils are slightly protuberant, and are directed anterolaterally at a point below the anterior terminus of the canthus rostralis directly above the anterior margin of the lower jaw. The diameter of the eye is slightly less than its distance from the nostril. The tympanum is broadly elliptical in an anterodorsal-posteroventral axis, and is separated from the eye by a distance about two-thirds of the length of the tympanum. The tympanic annulus is distinct and smooth. A bony supratympanic crest extends in an anterior-posterior plane to the level of the posterior edge of the tympanum. A slightly elevated transverse occipital crest is continuous with the posterior ends of the supratympanic crests.

The arm is rather slender, and bears a row of small subconical ulnar tubercles. The hand is large. The fingers are moderately long and unwebbed. The discs are small and round; the width of the disc on the third finger is about half the length of the tympanum. The relative lengths of the fingers are I > II < IV < III. The subarticular tubercles are small and subconical; supernumerary tubercles are absent. The palmar tubercle is low and bifid; the prepollical tubercle is elongate and elevated; in breeding males the median edge of the prepollical tubercle bears a brown nuptial excrescence. The hind limb is moderately slender. The tibia length is about 45% of the snout–vent length; the foot length is about 40% of the snout–vent length. A calcar and tarsal fold are absent; there is a row of low conical tubercles on the ventral surface of the tarsus. The outer metatarsal tubercle is small and conical; the inner metatarsal tubercle is elliptical, elevated, oriented diagonally, and visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. The inner toes are webbed basally; the webbing formula for the outer toes is **IV**(3–3½)—2½**V**. The subarticular tubercles are small and subconical; the supernumerary tubercles are limited to one each on the proximal segments of the third and fourth toes.

The skin on the dorsum is weakly granular; all skin on the head (except the eyelids) is co-ossified with the underlying cranial elements; the skin on the flanks, belly, and posteroventral surfaces of the thighs is more coarsely granular; the other ventral surfaces are smooth. There is a pair of subconical tubercles ventrolateral to the cloacal opening. The pouch opening is broadly V-shaped, with the anterior margin at the level of the posterior edge of sacrum. The dentigerous processes of the vomers are posteromedially inclined, and narrowly separated medially between the small ovoid choanae. Each process bears seven to nine teeth.

COLOR IN PRESERVATIVE

The dorsum is uniformly pale tan (42% of the specimens), tan with darker brown markings consisting of irregular spots (25%), or with the spots coalesced to form irregular paravertebral marks on the occiput and anterior part of the body (33%). A broad dark brown canthal stripe narrowly borders the lower edge of the orbit, and is continuous with a postorbital stripe that extends onto the flank. There is a broad dark brown sub-

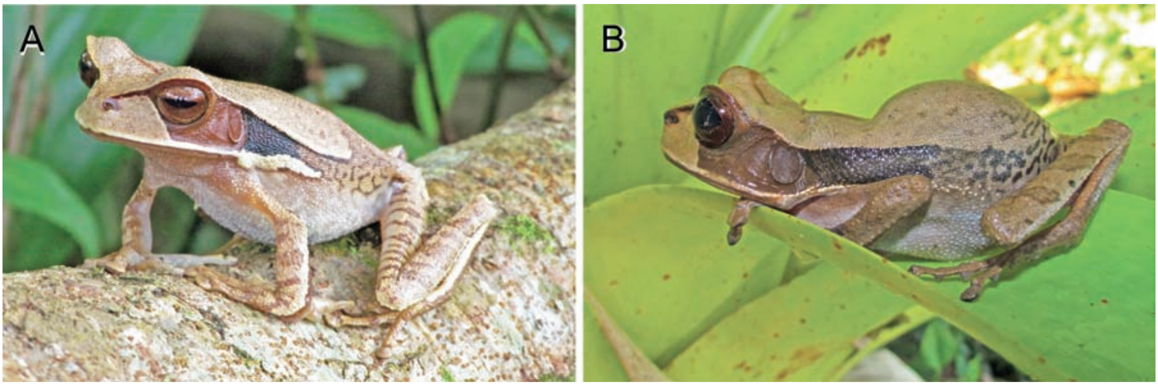

Fig. 10.2 *Gastrotheca fissipes*. A: Male. B: Brooding female. Both from Reserva Ecología da Michelin, Bahia, Brazil. Photos by C. V. de Mira Mendes, KUDA.

orbital bar; otherwise the side of the head is pale tan. The flanks are creamy tan to pale brown, with darker brown spots. The dorsal surfaces of the limbs have dark brown transverse bars. The anterior surfaces of the thighs are tan, and the posterior surfaces are brown, with cream flecks. The toes and webbing are tan.

COLOR IN LIFE

I have not observed living individuals of this species, but color photographs of specimens from the Reserva Ecología da Michelin, Bahia, Brazil, show the dorsum to be tan to brown, with darker brown markings, and the venter to be dull white (Fig. 10.2). The labial stripe, which extends onto the anterior part of the flank, is white to dull cream. The facial markings, including the tympanum, are dark brown, whereas the continuing dark mark on the flanks is nearly black. The iris is dark brown.

MEASUREMENTS

The single known female is much larger than any males I have examined. Measurements of eight males (Teixeira et al., 2012) fall within the range of males that I have examined (Table 10.1).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous fine pit-and-ridge pattern. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange and an otic flange that is complete to the head of the squamosal. The temporal arcade is complete, and covers the entire otic region. The specimen examined is a tomograph; thus it is not possible to discern some details with certainty. Because the frontoparietal covers the anterior epiotic eminence, along with the anterior part of the posterior epiotic eminence, it may be fused to them; the condition of the carotid canal is unknown. The alary processes of the premaxillae are nearly vertical (i.e., ≤ 10°); the premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for about half the length of the rostrum. The pars facialis of the maxilla is distinctly separated from the alary process of the premaxilla, and has only a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The postorbital process of the maxilla is massive and high; it forms the posteroventral margin of the orbit, and has a broad diagonal articulation with the broad but moderately short zygomatic process of the squamosal. The head of the squamosal bears a wide crest; the otic plate marginally articulates with the poorly ossified crista parotica. The proportions of the dorsal and ventral parts of the stapedial footplate could not be determined. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and terminates posterior to the level of the neopalatines; the shape of the terminus could not be determined. The endochondral sphenethmoid is not well ossified; it terminates anterior to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are moderately separated medially; each bears a well-developed irregular ventral flange. The pterygoid does not articulate with the squamosal, and lacks a dorsal ramus on its anterior ramus. The vomers bear moderately large dentigerous processes located between the middle quadrants of the choanae.

Table 10.1 Univariate statistics for adults of *Gastrotheca fissipes* and *G. megacephala*

		G. fissipes (4 males, 1 female)			*G. megacephala* (10 males, 5 females)		
Character	Sex	Mean	Range	SD	Mean	Range	SD
Snout–vent length	males	65.4	58.0–69.7	5.30	69.4*	60.0–77.8	5.64
	females	81.5	—	—	92.3*	78.7–110.0	13.24
Tibia length	males	30.7*	30.0–31.6	0.70	32.2*	29.2–36.5	2.37
	females	36.4*	—	—	42.9*	37.1–50.5	5.67
Foot length	males	26.3	25.2–27.9	1.16	27.6*	24.4–31.8	2.47
	females	29.9	—	—	39.4*	32.8–46.4	5.64
Head length	males	23.7§	23.0–25.0	0.91	25.3*	21.9–28.7	2.13
	females	27.0§	—	—	33.1*	28.5–40.0	4.47
Head width	males	25.7§	24.5–27.4	1.25	28.6*	24.3–31.5	2.71
	females	30.5§	—	—	37.4*	31.6–44.6	5.00
Interorbital distance	males	10.8	9.8–11.3	0.71	11.9*	8.0–14.2	1.90
	females	12.2	—	—	16.3*	14.0–18.7	2.33
Eyelid width	males	5.4	4.8–5.9	0.56	5.9§	4.8–6.9	0.74
	females	5.4	—	—	7.1§	5.3–8.0	1.10
Internarial distance	males	4.6	4.0–4.8	0.38	4.4*	3.8–4.9	0.36
	females	4.8	—	—	5.9*	5.0–6.9	0.78
Eye diameter	males	7.2	6.9–7.4	0.22	7.3*	6.5–8.0	0.56
	females	7.6	—	—	8.8*	7.7–10.2	10.5
Eye–nostril distance	males	5.9	5.7–6.0	0.13**	7.4*	6.3–9.2	0.83
	females	6.0	—	—	10.0*	8.0–12.0	1.77
Orbit–jaw distance	males	4.4	3.8–4.9	0.53	4.3*	3.1–5.5	0.62
	females	5.0	—	—	5.6*	4.8–6.7	0.69
Nostril–jaw distance	males	4.6	4.5–4.8	0.14	5.0*	4.0–6.0	0.68
	females	5.1	—	—	6.1*	5.4–7.2	0.73
Tympanum diameter	males	5.3	4.7–5.6	0.42	5.2§	4.0–6.5	0.75
	females	5.5	—	—	6.5§	5.4–7.4	0.90
Thumb length	males	15.7	14.9–16.4	0.65†	14.6*	12.9–16.0	0.91
	females	16.0	—	—	20.0*	16.6–22.2	2.51
Third finger length	males	19.3§	18.3–20.7	1.08	20.5*	15.5–23.5	2.30
	females	24.2§	—	—	29.7*	24.7–36.3	5.06
Disc width	males	2.7	2.5–3.0	0.22†	3.4*	2.4–4.3	0.58
	females	3.3	—	—	5.3*	3.7–6.3	1.01

§Differences between the means of the sexes are significant (ANOVA, $P \leq 0.05$).

*Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

†Differences between the means of the species are significant (ANOVA, $P \leq 0.05$).

**Differences between the means of the species are significant (ANOVA, $P \leq 0.01$).

Life History

The only brooding female specimen is the holotype, which has a snout–vent length of 81.5 mm; it contained 16 eggs, each about 10 mm in diameter. The number and size of the ova indicate that the eggs undergo direct development. Mendes et al. (2012) reported that in southern Bahia, males, usually situated higher than 4 meters above the ground, call from branches of trees, but according to Teixeira et al. (2012), Mendes at al. (2012) misidentified the frogs, which actually are *Gastrotheca recava*.

Advertisement Call

According to Teixeira et al. (2012), the call reported by Mendes et al. (2012) as that of *Gastrotheca fissipes* actually is the call of *G. recava*.

Distribution and Ecology

Gastrotheca fissipes is restricted to coastal regions of eastern Brazil, from Pernambuco to central Bahia (Fig. 10.3). The limited ecological data indicate that the species inhabits restinga vegetation, where individual have been found in an arboreal bromeliad (data

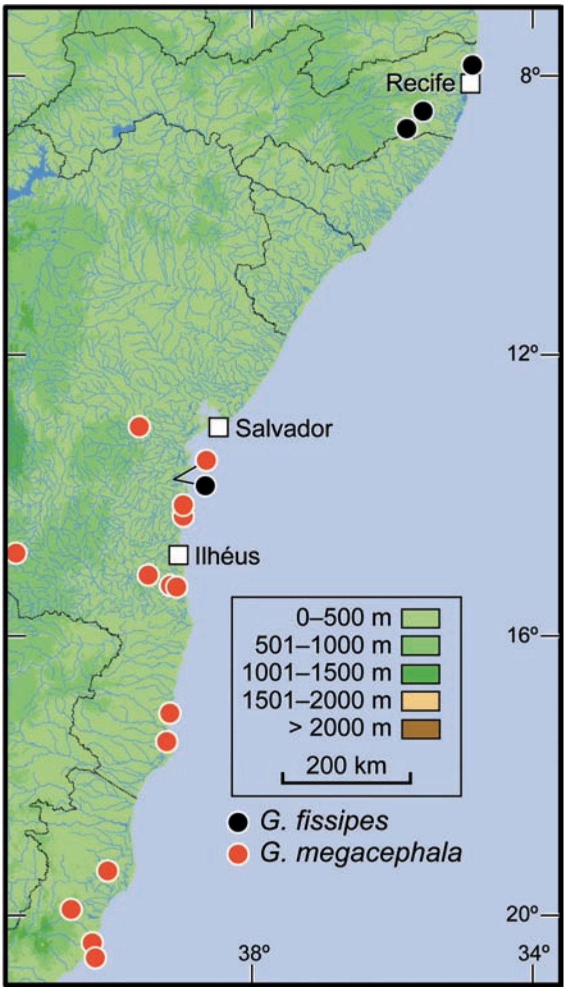

Fig. 10.3 Eastern Brazil, showing the localities of known occurrences of *Gastrotheca fissipes* and *G. megacephala*.

accompanying the holotype) and on branches of trees.

Conservation Status

In the International Union for Conservation of Nature (IUCN) Red List, *Gastrotheca fissipes* is categorized as a species of Least Concern, but this assessment also includes *G. megacephala* and *G. recava*; therefore the status of *G. fissipes* probably should be categorized as Data Deficient.

Etymology

Although not so stated by Boulenger (1888), the specific name apparently was derived from the Latin *fissus*, meaning "split," and the Latin *pes*, meaning "foot"; presumably the name was used in reference to the long toes that have only basal webbing.

Remarks

As noted by Izecksohn et al. (2009), earlier workers (e.g., Duellman, 1984) did not differentiate the specimens from Bahia, which Izecksohn et al. named *Gastrotheca megacephala*. Moreover, Mendes et al. (2012) confused *G. fissipes* with an unnamed species subsequently described as *G. recava* (Teixeira et al., 2012).

Gastrotheca (*Eotheca*) *flamma* Juncá and Nunes

Gastrotheca flamma Juncá and Nunes, 2008:62.—Holotype: MZUEFS 657 from Serra da Jibóia, 850 m, Municipality of Santa Terezinha, Estado do Bahia, Brazil.

Diagnosis

In this medium-sized species, the only known female has a snout–vent length of 55.3 mm. The tibia length is 50% of the snout–vent length, and is much longer than the foot. The interorbital distance is about twice the width of the upper eyelid. The skin on the dorsum is weakly granular, adherent to but not co-ossified with the skull, and lacks transverse ridges. Two conical tubercles are present on the outer edge of the upper eyelid. An elongately triangular calcar is present on the heel. The tympanic annulus is granular. The first finger is much longer than the second. The discs on the fingers are much wider than the digits proximal to the discs. The fingers are webbed basally; on the foot the webbing extends to the penultimate subarticular tubercle on the fourth toe and the distal subarticular tubercle on the fifth toe. The dorsum is reddish tan, with irregular dark brown markings. Markings on the head consist of a dark brown interorbital bar, a transverse bar anterior to the orbits, and diffuse labial bars. A pale dorsolateral stripe is absent. The flanks are colored like the dorsum; the venter is beige.

The presence of two conical tubercles on the margin of the upper eyelid distinguishes *Gastrotheca flamma* from all other members of the genus. Several species (e.g., *G. andaquiensis* and *G. cornuta*) in northwestern South America have one larger fleshy triangular projection on each eyelid, and *G. pulchra* has a single smaller tubercle on each eyelid. Among the species of *Gastrotheca* in eastern and southeastern Brazil, only *G. flamma* and *G. pulchra* have calcars, but these species differ in that *G. pulchra* has smooth skin on the dorsum, in contrast to granular skin in *G. flamma*, which is also much larger (55 mm in snout–vent length) than *G. pulchra* (34 mm). In addition to the absence of enlarged tubercles on the eyelids and calcars, *G. albolineata* and *G. microdiscus* differ from *G. flamma* by the former two species having a distinct broad white dorsolateral stripe. *G. ernestoi* and *G. fulvorufa* have slight co-ossification in the frontoparietal region, but neither has eyelid tubercles or calcars. The other Brazilian species (*G. fissipes*, *megacephala*, *prasina*, and *recava*) have extensive cranial co-ossification, are much larger, and have only basal webbing between the toes.

Description

The following description is based on one adult female. The body is moderately robust; the maximum known snout–vent length is 55.3 mm in a female. The head is about as wide as long, and as wide as the body. The snout is truncate in dorsal view and in profile. The canthus rostralis is straight, slightly elevated, and angular in cross-section. The loreal region is concave; the lips are rounded. The internarial region is slightly depressed. The nostrils are barely protuberant, and are directed laterally at a level behind the anterior margin of the jaw. The diameter of the eye is about equal to its distance from the nostril. The tympanum is round, and separated from the eye by a distance nearly twice the diameter of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately heavy and granular; it extends from the posterior corner of the orbit to a point posterior to the insertion of the arm, and barely obscures the upper edge of the tympanum.

The arm is robust, with a row of subconical ulnar tubercles. The hand is large, with a crenulated fold along the outer edge of the fourth finger. The fingers are long, and webbed basally. The discs are large, round, and about twice as wide as the digits proximal to the discs; the width of the disc on the third finger is slightly greater than the diameter of the tympanum. The relative lengths of the fingers are I > II < IV < III. The subarticular tubercles are large and round; supernumerary tubercles are absent. The palmar tubercle is low and bifid; the prepollical tubercle is large, elongately ovoid, and elevated; the condition of nuptial excrescences is unknown. The hind limb is moderately long and slender. The tibia length is 50.4% of the snout–vent length; the foot length is 38.2% of the snout–vent length. The heel bears a distinct triangular calcar; there is a row of low subconical tubercles on the outer edge of the tarsus, and a crenulated fold on the other edge of the foot and fifth toe. Tarsal folds and an outer metatarsal tubercle are absent; the inner metatarsal tubercle is ovoid, and is visible from above. The toes are moderately long and robust. The relative lengths of the toes are I < II < V < III < IV. The toes are about two-thirds webbed; the webbing formula is **I**2—2**II**1—2½**III**11—2^{-}**IV**1½—1**V**. The subarticular tubercles are moderately small and round; the supernumerary tubercles are small, and present on the proximal segments of the fourth and fifth toes.

The skin on the dorsum is weakly granular, and is not co-ossified with the underlying cranial elements on the top of the head; the skin on the throat, belly, and undersurfaces of the thighs is coarsely granular; the other surfaces are smooth. Cloacal folds and tubercles are absent. The opening of the brood pouch is broadly V-shaped, with the anterior border posterior to the level of the sacrum. The dentigerous processes of the vomers lie between the choanae. Each process bears three teeth.

COLOR IN PRESERVATIVE

The dorsum is tan, with brown interconnected X-shaped marks on the back. Brown markings on the head consist of an interorbital bar, a narrow transverse bar anterior to the orbits, and diffuse labial bars. There are no canthal or postorbital stripes. Narrow transverse dark brown bars are present on the limbs: three on the forearms, seven on the thighs, five on the shanks, and four on the tarsi. The flanks and posterior surfaces of the thighs are tan; the venter is cream, with small irregular brown marks on the throat.

COLOR IN LIFE

The dorsum is reddish tan, with dark brown markings on the head, body, and limbs as described above. The posterior surfaces of the thighs and the ventral surfaces of the body and limbs are orange beige, with reddish brown marks on the throat (Juncá and Nunes, 2008). The iris is deep copper (Fig. 10.4).

MEASUREMENTS

The only known specimen is a female, with the following measurements (in mm): snout–vent length 55.3, tibia length 26.8, foot length 21.1, head length 20.0, head width 20.3, interorbital distance 7.0, upper eyelid width 4.7, internarial distance 3.4, eye diameter 5.3, eye–nostril distance 5.4, orbit–jaw distance 3.0, nostril–jaw distance 4.2, tympanum diameter 3.8, thumb length 11.6, third finger length 14.8, and width of disc on third finger 3.4.

CRANIAL OSTEOLOGY

Nothing is known.

Life History

Nothing is known. Presumably *Gastrotheca flamma* is like other members of the subgenus *Eotheca* in having large eggs that hatch as froglets.

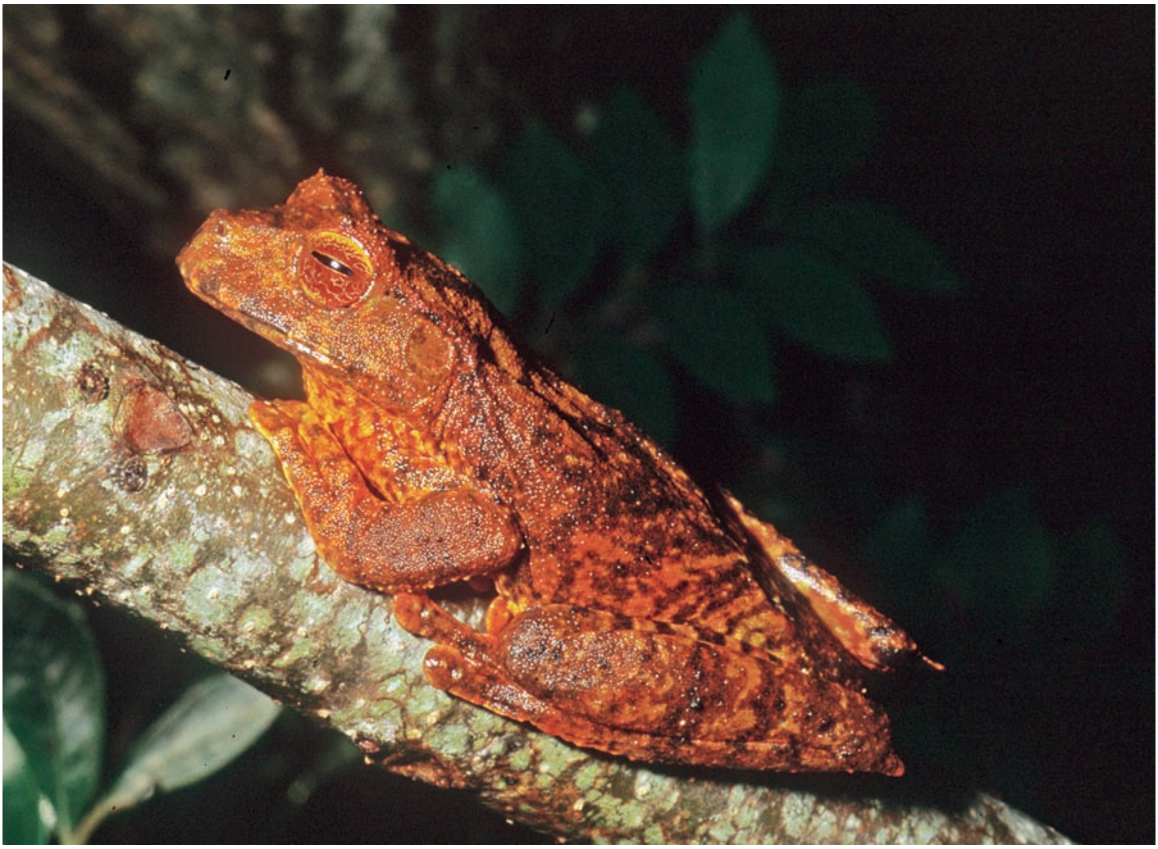

Fig. 10.4 *Gastrotheca flamma* (MZUEFS 657, holotype), female, 53 mm SVL, from Serra da Jibóia, Bahia, Brazil. Photo by I. Nunes, KUDA.

Distribution and Ecology

This species is known only from the type locality, at an elevation of 850 m in the Serra da Jibóia in Bahia, eastern Brazil (Fig. 10.3). According to Juncá (2006), the region of the type locality is within the ecotone between the Atlantic rainforest and the open dry forest (Caatinga).

Conservation Status

This species is known only from the Serra da Jibóia, in the semiarid region, as defined by Camardelli and Napoli (2012). Known only from a single specimen collected in 2001 and described in 2008, on the IUCN Red List this species must be declared Data Deficient.

Etymology

The specific name is a Latin noun in apposition, *flamma*, meaning "blaze" or "flame"; according to Juncá and Nunes (2008), the name alludes to the fire-like red dorsal coloration.

Remarks

Juncá and Nunes (2008) considered the skin on the head to be co-ossified with the underlying cranial elements, yet insertion of a probe revealed that the skin was adherent to but not co-ossified with the underlying bones. These authors also stated that the foot length of the holotype was 38.0 mm; this obviously was a measurement from the proximal edge of the astragalus-calcaneum to the tip of the fourth toe; my measurement from the proximal edge of the inner metatarsal tubercle to the tip of the fourth toe is 21.1 mm.

Gastrotheca (*Eotheca*) *megacephala* Izecksohn, Carvalho-e-Silva, and Peixoto

Gastrotheca fissipes (in part)—Duellman, 1984:303.

Gastrotheca megacephala Izecksohn, Carvalho-e-Silva, and Peixoto, 2009:83.—Holotype: ZUFRJ 7223 from Restinga da Lagoa do Milho, Guarapari, Estado do Espírito Santo, Brazil.

Diagnosis

Adults of this large species attain a snout–vent length of 110 mm. The tibia length is less than 50% of the snout–vent length, and is slightly longer than the foot. The interorbital distance is about twice the width of the upper eyelid. The skin on the dorsum is finely granular in males, and smooth in females; it is co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is much longer than the second. The discs on the fingers are much wider than the digits. The fingers are unwebbed; on the foot the webbing is basal between Toes III and IV and between Toes IV and V. The dorsum is tan to pale brown, with or without slightly darker diffuse brown spots. Markings on the head consist of a dark brown canthal stripe and broad subocular bar. A pale dorsolateral stripe is absent. The flanks are dark brown; the venter is dull creamy tan.

Gastrotheca megacephala is like *G. fissipes*, *prasina*, and *recava* in having an extensively co-ossified skull. *G. megacephala* differs from *G. fissipes* by lacking chevron-shaped marks on the dorsum, and by having a different configuration of the posterior end of the skull. In all of these species except *G. recava*, the bony supratympanic crest extends to the level of the posterior edge of the tympanum; in *G. fissipes* the posterior margin of the skull is scalloped, and lacks a transverse occipital crest, which is evident and continuous with the supratympanic crests in *G. megacephala* and *G. prasina*. *G. recava* differs from *G. megacephala* by lacking a broad brown labial bar below the orbit; instead, the entire labial and postorbital regions are dark brown, a color continuous onto the flanks. Furthermore, the configuration of the cranial roofing bones is distinctly different; the frontoparietals have a narrow articulation with the squamosal, in contrast to the broad articulation in *G. megacephala*; also, the dermal sphenethmoid is much smaller than that in *G. recava*. *G. megacephala* differs from the smaller *G. flamma* and *G. pulchra* by lacking calcars and tubercles on the eyelids.

Description

The following description is based on 15 adults. The body is robust; males attain a snout–vent length of 77.8 mm, and 110 mm in females. The head is much wider than long, but not as wide as the body. The snout is narrowly truncate terminally, but bluntly rounded in general shape, and high and truncate in profile. The canthus rostralis is acutely angular in cross-section. The loreal region is nearly flat; the lips are slightly rounded. The top of the head is flat. The interorbital distance is slightly less than twice the width of the upper eyelid. The internarial area is slightly depressed. The nostrils are not protruding, and directed laterally at a point below the anterior terminus of canthus rostralis directly above the anterior margin of the lower jaw. The diameter of the eye is slightly less than its distance from the nostril. The tympanum is broadly elliptical in an anterodorsal-posteroventral axis, and separated from the eye by a distance about two-thirds the length of the tympanum. The tympanic annulus is distinct and smooth. A bony supratympanic crest extends in an anterior-posterior plane to the level of the posterior edge of the tympanum. A slightly elevated transverse occipital crest is continuous with the posterior ends of the supratympanic crests.

The arm is rather robust, and lacks a row of distinct ulnar tubercles. The hand is large. The fingers are moderately long and unwebbed. The discs are large and round; the width of the disc on the third finger is about two-thirds the length of the tympanum. The relative lengths of the fingers are I > II < IV < III. The subarticular tubercles are large and round; supernumerary tubercles are absent. The palmar tubercle is small and round; the prepollical tubercle is elongate and elevated; in breeding males the median edge of the prepollical tubercle bears a brown nuptial excrescence. The hind limb is moderately slender. The tibia length is less than 50% of the snout–vent length; the foot length is less than 44% of the snout–vent length. A calcar and tarsal fold are absent; there are two rows of small conical tubercles on the ventral surface of the tarsus. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is small, ovoid, and not visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. The inner toes are not webbed; the outer toes are webbed basally. The subarticular tubercles are small and subconical; supernumerary tubercles are present only on the proximal segments of the third and fourth toes.

The skin on the dorsum is finely granular in males, and smooth in females; all skin on the head (except the eyelids) is co-ossified with the underlying cranial elements; the skin on the flanks, belly, and posteroventral surfaces of the thighs is granular; the other ventral surfaces are smooth. One to three pairs of subconical tubercles are present ventrolateral to the cloacal opening. The pouch opening is broadly V-shaped, with the anterior margin at the level of the posterior edge of sacrum. The dentigerous processes of the vomers are posteromedially inclined, and are narrowly separated medially between the small ovoid choanae. Each process bears six to nine teeth.

COLOR IN PRESERVATIVE

The dorsum is uniformly pale tan, with or without diffuse irregular slightly darker spots; two individuals have small cream spots. A narrow dark brown canthal stripe and broad dark brown suborbital bar are present on the otherwise tan facial region. A dark brown postorbital stripe broadens to encompass the tympanum, and continues across the flank to the groin. Ventrally the flanks are creamy tan to pale brown, with darker brown spots. The dorsal surfaces of the limbs are tan, with dark brown transverse bars: two or three on the forearm, four to seven on the thigh, three or four on the shank, and four or five on the tarsus. The anterior surfaces of the thighs are tan; the posteroventral surfaces are brown, with cream flecks. The toes and webbing are tan.

COLOR IN LIFE

Photographs of two individuals show a tan dorsum, with or without faintly darker markings on the body (Fig. 10.5). The bars on the limbs are dark brown. Darker brown facial markings consist of an irregular mark that begins just posterior to the nostrils, and is continuous or not to the orbit, below which there is a broad suborbital bar. A dark brown postorbital stripe broadens to encompass the tympanum, and continues as a broad stripe onto the flanks. This stripe either continues to the groin or terminates at midflank; in the latter case, there are two or three dark brown vertical marks or a series of irregular black spots on the posterior part of the flanks, which are dull tan. The iris is bronze brown, with fine black flecks.

MEASUREMENTS

Males of this large species attain a maximum snout–vent length of 77.8 mm, and 110 mm in females. Measurements of 10 males and 5 females are given in Table 10.1. Four juveniles and subadults have snout–vent lengths of 27.7 mm, 34.4 mm, 43.3 mm, and 63.9 mm.

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous fine pit-and-ridge pattern. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange and a moderate-sized otic flange. A temporal arcade is present. The frontoparietal covers the anterior epiotic eminence, along with the anterior part of the posterior epiotic eminence, and is partially fused to them; hence the carotid canal is partially closed, and exits the skull posteriorly adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are nearly vertical (i.e., ≤ 10°); the premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for about half the length of the rostrum. The pars facialis of the maxilla is distinctly separated from the alary process of the premaxilla, and has only a narrow overlap with the dental process of the premaxilla. The

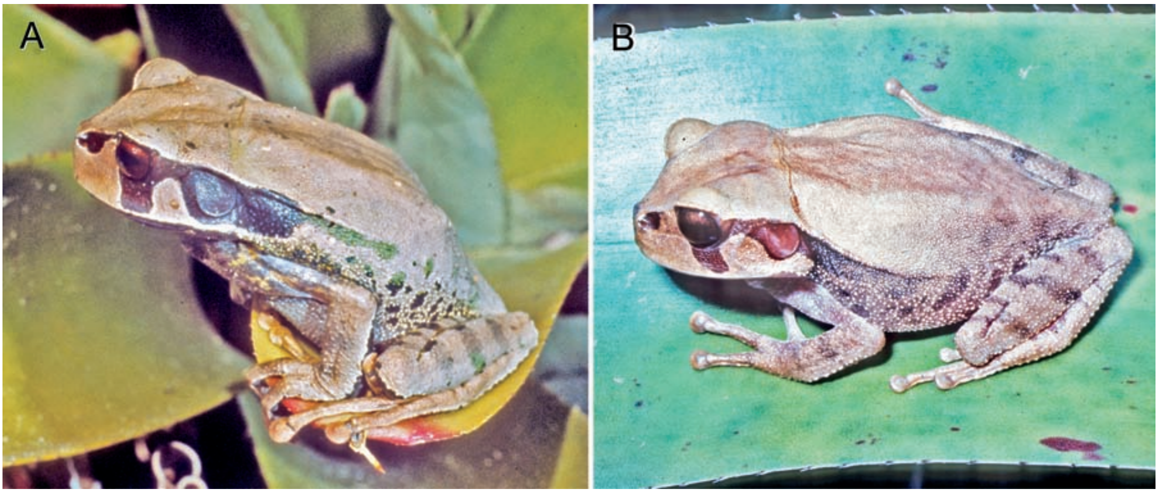

Fig. 10.5 *Gastrotheca megacephala*. A. Santa Teresa, Espírito Santo, Brazil. B. Vilha Velha, Espírito Santo, Brazil. Photos by W. C. A. Bokermann, KUDA.

quadratojugal is long. The postorbital process of the maxilla is massive, and has a broad horizontal articulation with the wide zygomatic process of the squamosal. The head of the squamosal bears a wide crest; the otic plate completely articulates marginally with the crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in size, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has a blunt terminus anterior to the level of the neopalatines. The sphenethmoid is ossified posterior to the midlength of the orbit, and synostosed with the prootic. The neopalatines are narrowly separated medially, and lack ventral ridges. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a distinct long blunt-tipped dorsal ramus on its anterior arm. The vomers bear moderately large dentigerous processes located between the anterior quadrants of the choanae.

Life History

Gastrotheca megacephala produces eggs that undergo direct development. Izecksohn et al. (2009) reported on two females that each contained 17 eggs.

Advertisement Call

According to Izecksohn et al. (2009), the call consists of two notes. The first note has a duration of about 200 milliseconds and has nine pulses; the second note is more intense, with five pulses contained in a period of about 100 milliseconds. The interval between the notes is about 60 milliseconds. The dominant frequency is between 1400 and 1500 Hz.

Distribution and Ecology

This large species inhabits bromeliads in the forests on the coastal lowlands and in the restinga along the coast from central Bahia into Espírito Santo, Brazil (Fig. 10.3). In the forest, the frogs call from the canopy, but in the restinga they are just a few meters above the ground when calling from bromeliads.

Conservation Status

There has been no critical assessment of the conservation status of *Gastrotheca megacephala*, which formerly was confused with *G. fissipes*. Inasmuch as this species is restricted to the coastal forests, it probably should be categorized as Vulnerable on the IUCN Red List.

Etymology

The specific name is derived from the Greek *mega*, meaning "large," and the Greek *kephale*, meaning "head." As stated by Izecksohn et al. (2009), the name refers to the large head of this species.

Remarks

Gastrotheca fissipes, identified by Boulenger (1888), differed from other Brazilian species subsequently discovered and was described as having a large casqued head, with the skin co-ossified with the underlying roofing bones, and reduced webbing on the hands and feet. Several authors (e.g., Duellman, 1984) examined only a few specimens and considered all large *Gastrotheca* with casqued heads to be *G. fissipes*, which was thought to range from Pernambuco to Espírito Santo. Examination of many more specimens by Izecksohn et al. (2009) revealed that specimens from Bahia and Espírito Santo differed from those in Pernambuco in head width, posterior edge of the casque, and coloration. Thus they recognized two species, the southern one of which they named *G. megacephala*.

Gastrotheca (*Eotheca*) *prasina* Teixeira, Vechio, Recoder, Carnaval, Strangas, Damasceno, Sena, and Rodrigues

Gastrotheca prasina Teixeira, Vechio, Recoder, Carnaval, Strangas, Damasceno, Sena, and Rodrigues, 2012:5.—Holotype: MZUSP 147059 from Reserva Biológica da Mata Escura, Município de Jequitinhonha, Estado do Minas Gerais, Brazil.

Diagnosis

Adults of this species attain a maximum snout–vent length of 97.2 mm. The tibia length is less than 50% of the snout–vent length, and is much shorter than the foot. The interorbital distance is more than twice the width of the upper eyelid. The skin on the dorsum is shagreen, co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is longer than the second. The discs are twice the width of the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing is basal between the fourth and fifth toes. The dorsum is pale green, with pale tan suffusions in the occipital and sacral regions. Markings on the head consist of a dark brown suborbital bar and dark brown postorbital stripe. A pale dorsolateral stripe is absent. The flanks are mottled tan and black; the venter is dark gray.

Four species of *Gastrotheca* in northeastern Brazil differ from all other members of the genus by having broad heads, with the roofing bones of the skull co-ossified with the overlying skin. Among these species, *G. prasina* is unique in having a green dorsal ground color, whereas the dorsum is brown in the other species. The posterior border of the skull is approximately straight in *G. megacephala* and *G. prasina*, in contrast to the scalloped or indented margins in *G. fissipes* and *G. recava*; furthermore, *G. prasina* can be distinguished from the latter two species by having a broad suborbital bar (absent in *G. recava*). Two other species, *G. flamma* and *G. pulchra*, differ from *G. prasina* by having calcars on the heels and tubercles of the margin of the upper eyelids.

Description

The following description is based on two adults, plus information from the original description (Teixeira et al., 2012). The body is robust; males of this large species attain a snout–vent length of 89.5 mm; the only known female has a snout–vent length of 97.2 mm. The snout is narrowly truncate terminally, but acutely rounded in general shape, and is high and truncate in profile. The canthus rostralis is acutely angular in cross-section. The loreal region is concave; the lips are narrowly rounded. The top of the head is flat. The interorbital distance is about twice the width of the upper eyelid. The internarial area is slightly depressed. The nostrils are not protruding, and are directed laterally at a point below the anterior terminus of canthus rostralis slightly posterior to the anterior margin of the lower jaw. The diameter of the eye is about equal to its distance from the nostril. The tympanum is broadly elliptical in a vertical axis, and is separated from the eye by a distance about equal to the length of the tympanum. The tympanic annulus is distinct and smooth. A bony supratympanic crest extends in an anterior-posterior plane to the level of the posterior edge of the tympanum. An elevated transverse occipital crest is absent.

The arm is rather robust, and has a row of minute ulnar tubercles. The hand is large. The fingers are moderately long and unwebbed. The discs are large and round; the width of the disc on the third finger is greater than the length of the tympanum. Finger I is much longer than Finger II. The relative lengths of the fingers are I > II < IV < III. The subarticular tubercles are small and round; supernumerary tubercles are absent. The palmar tubercle is small and round; the prepollical tubercle is elongate; in breeding males the median edge of the prepollical tubercle bears a brown nuptial excrescence. The hind limb is moderately slender. The tibia length is less than 55% of the snout–vent length; the foot length is less than 45% of the snout–vent length. A calcar and tarsal fold are absent. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is small, ovoid, and not visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. The inner toes are not webbed; the outer toes are webbed basally. The subarticular tubercles are small and round; supernumerary tubercles are minute or absent.

The skin on the dorsum is shagreen; all skin on the head (except the eyelids) is co-ossified with the underlying cranial elements; the dorsal surfaces of the hind limbs are weakly granular; the skin on the flanks, belly, and posteroventral surfaces of the thighs is granular; the other ventral surfaces are smooth. Two pairs of subconical tubercles are present, ventrolateral to the cloacal opening. The pouch opening is broadly V-shaped, with the anterior margin at the level of the posterior edge of the sacrum. The dentigerous processes of the vomers are nearly transverse, and are widely separated medially between the large ovoid choanae. Each process bears six to eight teeth.

COLOR IN PRESERVATIVE

The dorsal surfaces of the head and body are dull gray; the lower flanks and the posterior surfaces of the thighs are mottled black and tan. A dark brown suborbital bar and postorbital stripe are evident, as are dark gray transverse bars on the thighs. The ventral surfaces of the belly and hind limbs are dull brown, with white-tipped granules. The vocal sac in males is black.

COLOR IN LIFE

The dorsal surfaces of the body and head are green, with a suffusion of tan laterally in the sacral region and transversely in the occipital region (Fig. 10.6). There may be a middorsal mark extending posteriorly from the interorbital region. The flanks are black, with white flecks. The dorsal surfaces of the thigh and shank are tan, with green transverse bars; the anterior surfaces of the thighs are tan, with black bars; the posterior surfaces are black, with cream mottling. Markings on the head consist of a narrow orange-tan canthal stripe that continues on the outer edge of the eyelid to about midlength of the body. Dark brown markings consist of a broad suborbital bar and a postorbital stripe that is continuous posteriorly below the orange-tan stripe. The throat and chest are dark gray; the belly is pale gray, with dark gray reticulations laterally. The ventral surfaces of the hind limbs are dark gray, with pale mottling. The subcloacal region is black, with white tubercles. The iris is dark reddish bronze.

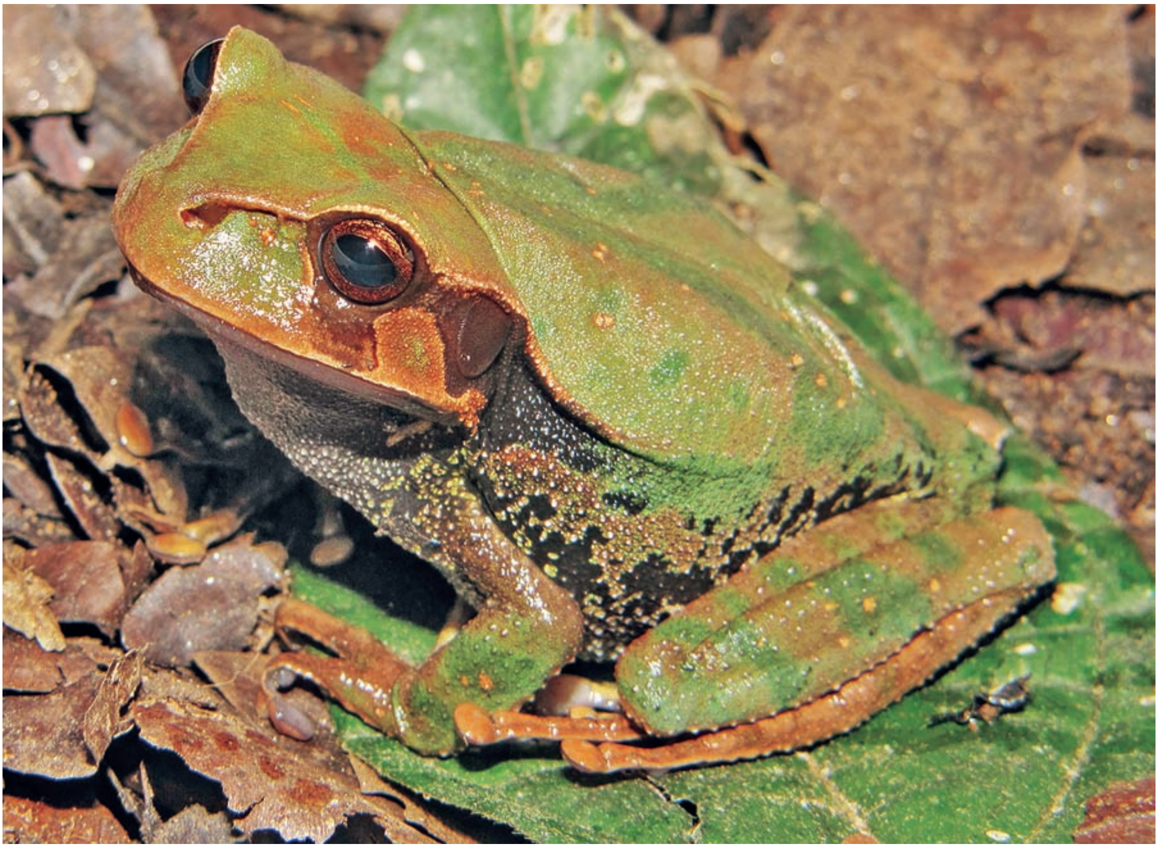

Fig. 10.6 *Gastrotheca prasina* (MZUSP 147059), male, 83.0 mm SVL, from Reserva Biológica da Mata Escura, Município de Jequitinhonha, Minas Gerais, Brazil. Photo by M. Teixeira Jr., KUDA.

MEASUREMENTS

The single known female is much larger than the largest male (Table 10.2).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous semicoarse pit-and-ridge pattern. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange, and has an otic flange that is complete to the squamosal to form a complete temporal arcade. The frontoparietal covers the anterior epiotic eminence and the anterior part of the posterior epiotic eminence, and is fused to them; hence the carotid canal is closed, and exits the skull posteriorly adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are nearly vertical (i.e., ≤ 10°); the premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for only about 25% of the length of the rostrum. The pars facialis of the maxilla is distinctly separated from the alary process of the premaxilla, and has only a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The postorbital process of the maxilla is massive, and has a broad horizontal articulation with the wide zygomatic process of the squamosal. The head of the squamosal lacks a crest; the otic plate marginally articulates with the crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in size, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has a blunt terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are narrowly separated medially, and bear ventral flanges. The pterygoid articu-

Table 10.2 Measurements of *Gastrotheca prasina* and *G. recava*. Measurements are from Teixeria et al. (2012).

		G. prasina (6 males, 1 female)		*G. recava* (14 males, 7 females)	
Character	Sex	Mean	Range	Mean	Range
Snout–vent length	males	83.7	79.2–89.5	65.8	57.0–75.4
	females	97.2	—	76.0	67.2–84.9
Tibia length	males	38.2	35.5–40.4	34.4	31.1–38.8
	females	41.4	—	40.0	37.0–43.1
Foot length*	males	34.0	—	26.1	25.2–28.9
	females	36.8	—	34.5	—
Head length	males	29.5	27.6–32.2	23.5	20.7–26.1
	females	32.8	—	27.0	24.3–29.4
Head width	males	32.4	31.0–34.9	26.1	22.3–29.6
	females	36.5	—	30.7	27.8–32.2
Interorbital distance	males	6.3	5.9–6.9	6.9	6.0–8.0
	females	15.7	—	7.4	7.1–8.9
Eyelid width*	males	7.2	—	6.4	5.8–7.2
	females	7.4	—	7.0	—
Internarial distance*	males	5.3	—	4.5	4.0–5.5
	females	6.1	—	4.7	—
Eye diameter	males	7.2	6.4–7.9	7.3	6.4–8.4
	females	8.1	—	7.6	6.5–8.7
Eye–nostril distance	males	8.7	8.1–9.4	6.2	5.8–7.2
	females	9.6	—	7.3	6.2–8.2
Orbit–jaw distance*	males	4.7	—	3.7	3.3–4.1
	females	4.9	—	4.7	—
Nostril–jaw distance*	males	6.1	—	4.6	3.8–5.5
	females	6.0	—	5.4	—
Tympanum diameter	males	6.1	5.5–6.8	5.9	5.0–6.6
	females	6.7	—	6.6	5.9–7.8
Thumb length*	males	17.0	—	14.7	13.0–15.5
	females	19.5	—	20.1	—
Third finger length*	males	26.2	—	21.1	19.2–24.6
	females	26.8	—	29.3	—
Disc width	males	4.7	4.3–5.0	3.5	3.0–4.1
	females	4.6	—	4.1	3.1–4.8

*Measurements taken by Duellman for one male and one female of *G. prasina*, and for five males and one female of *G. recava*.

lates with the medial surface of the zygomatic ramus of the squamosal via a distinct long blunt-tipped dorsal ramus on its anterior arm. The vomers bear moderately large dentigerous processes located between the anterior quadrants of the choanae.

Life History

The only known female has at least 16 large eggs in the pouch; thus this species most certainly undergoes direct development.

Advertisement Call

Teixeira et al. (2012) reported that the call usually consists of two notes: the first note is 432–543 milliseconds ($\bar{x} = 485$) in length, and the second note is 149–187 milliseconds ($\bar{x} = 172$) long. The dominant frequency of the first note is 1350–1405 Hz ($\bar{x} = 1370$); the second note is slightly lower, 1240–1550 Hz ($\bar{x} = 1331$). Occasionally only the first note is given.

Distribution and Ecology

This species is known only from the type locality, at an elevation of 989 m in northeastern Minas Gerais, Brazil (Fig. 10.7). The type locality is the summit of a hill in the Atlantic Coastal Forest, where the forest gives way to clearings with scattered small trees and clusters of terrestrial bromeliads growing on sandy soil. By day individuals take shelter in the bromeliads. Shortly after

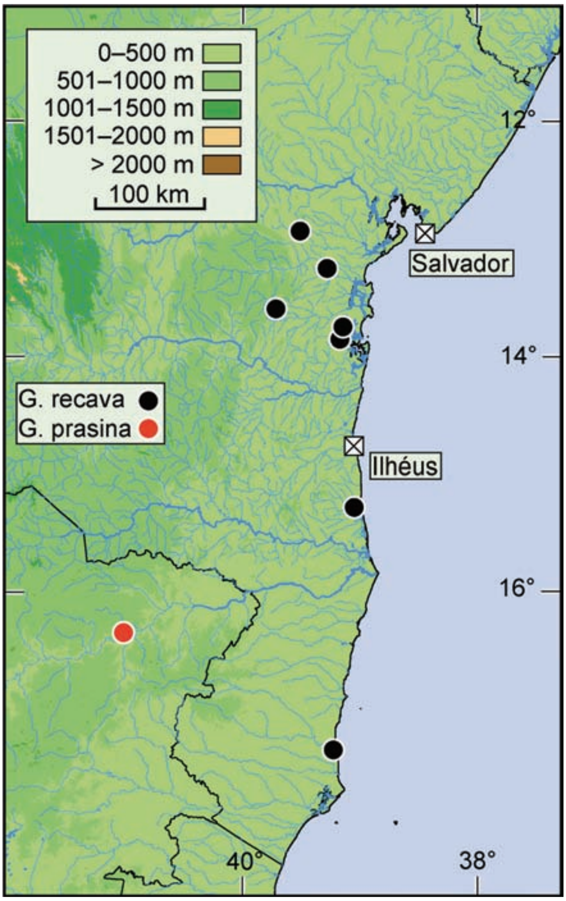

Fig. 10.7 Eastern Brazil, showing the localities of known occurrences of *Gastrotheca prasina* and *G. recava*.

dusk, males called from the bromeliads; later they ascended to heights of up to 3 m in the small trees to continue calling (Teixeira et al., 2012).

Conservation Status

This recently discovered species must be listed as Data Deficient on the IUCN Red List.

Etymology

According to the original description (Teixeira et al., 2012), the specific epithet is from the Latin *prasinus*, meaning "green"; the name refers to the general greenish color of the body.

Remarks

In a Bayesian inference tree based on molecular data for six species of *Gastrotheca* (Teixeira et al., 2012), *G. prasina* is the sister taxon to *G. megacephala*; *G. recava* is the sister taxon to those two species, whereas *G. fissipes* is the sister taxon to all three. In the phylogeny presented here, these four species of *Gastrotheca* are tightly grouped with *G. prasina* as the sister taxon to *G. fissipes* + *G. megacephala*, whereas the morphologically distinctive *G. recava* is the sister taxon to the other three species.

Gastrotheca (*Eotheca*) *pulchra* Caramaschi and Rodrigues

Gastrotheca pulchra Caramaschi and Rodrigues, 2007:9.—Holotype: MZUSP 85870 from Reserva Biológica de Pau Brasil, 15 km NW Porto Seguro, Estado do Bahia, Brazil.

Diagnosis

In this small species, females attain a maximum known snout–vent length of 36.8 mm, and 29.0 mm in males. The tibia length is more than 53% of the snout–vent length, and is longer than the foot. The interorbital distance is slightly greater than the width of the upper eyelid. The skin on the dorsum is smooth, not co-ossified with the skull, and lacks transverse ridges. A small tubercle is present on the outer edge of the upper eyelid. A triangular calcar is present on the heel. The tympanic annulus is smooth. The first finger is much longer than the second. The discs are much wider than the digits proximal to the discs. The outer fingers are webbed basally; on the foot the webbing extends to the penultimate subarticular tubercle on the fourth toe and the distal subarticular tubercle on the fifth toe. The dorsum is pinkish gray, with faintly darker chevron markings in the sacral region. Markings on the head consist of a gray-brown interorbital bar and a subocular bar. A pale dorsolateral stripe is absent; the venter is an immaculate white.

Relatively few species of *Gastrotheca* have a pronounced tubercle on the outer edge of the eyelid. *G. flamma* has two tubercles on each eyelid, and several species in northwestern South America (e.g., *G. andaquiensis* and *G. cornuta*) have one larger fleshy triangular projection on each eyelid. Among the species of *Gastrotheca* in eastern and southeastern Brazil, only *G. flamma* and *G. pulchra* have calcars, but these species differ in that *G. pulchra* has smooth skin on the dorsum, in contrast to granular skin in *G. flamma*, which is much larger (55 mm in snout–vent length) than *G. pulchra* (34 mm). No other Brazilian species has a tubercle on the eyelid and a calcar on the heel.

Description

The following description is based on eight specimens. The body is robust; the maximum known snout–vent length is 34.2 mm in females, and 29.0 mm in males. The width of the head is slightly greater than its length, and is about the same width as the body. The snout is nearly truncate in dorsal view, and is bluntly rounded in profile. The canthus rostralis is weakly curved, and is acutely rounded in cross-section. The loreal region is barely concave; the lips are rounded. The top of the head is slightly convex. The internarial region is flat. The nostrils are barely protuberant, and are directed anterolaterally well behind the anterior margin of the jaw. The interorbital distance is only slightly greater than the width of the upper eyelid. The diameter of the eye is about equal to its distance from the nostril. The tympanum is round, and is separated from the eye by a distance nearly twice the diameter of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is weak, extends from the posterior corner of the orbit to a point posterior to the tympanum, and barely obscures the upper edge of the tympanum.

The arm is moderately robust, and lacks ulnar tubercles. The hand is relatively small. The fingers are short and unwebbed. The round discs are about 1.5 times as wide as the digits proximal to the discs; the width of the disc on the third finger is slightly less than the diameter of the tympanum. The relative lengths of the fingers are I > II < IV < III. The subarticular tubercles are small and subconical; the supernumerary tubercles are subconical, and are prominent on the proximal segments of the digits. The palmar tubercle is low and bifid; the prepollical tubercle is large, elongately ovoid, and elevated; existing male specimens lack nuptial excrescences. The hind limb is moderately long and slender. The tibia length is about 58% of the snout–vent length; the foot length is 40%–47% of the snout–vent length. The heel bears a distinct triangular calcar; there is a row of low subconical tubercles on the outer edge of the tarsus. Tarsal folds and an outer metatarsal tubercle are absent; the inner metatarsal tubercle is ovoid, and is visible from above. The toes are moderately long and robust. The relative lengths of the toes are I < II < V < III < IV. The toes are about two-thirds webbed; the webbing formula is **I**2—2^{+}**II**1—2**III**1—2**IV**1½—1**V**. The subarticular tubercles are small and round; the supernumerary tubercles are small, and are present on the proximal segments of the fourth and fifth toes.

The skin on the dorsum is finely shagreen, and is not co-ossified with the underlying cranial elements on the top of the head; transverse dermal ridges are absent. The skin on the throat, belly, and undersurfaces of the thighs is coarsely granular; the other surfaces are smooth. Cloacal folds are absent; a pair of tubercles lies below the cloacal opening; below these is a row of four tubercles. The opening of the brood pouch is broadly V-shaped, with the anterior border posterior to the level of the sacrum. The dentigerous processes of the vomers are transverse, and are narrowly separated medially between the choanae. Each process bears four or five teeth.

COLOR IN PRESERVATIVE

The dorsum is tan, with or without faint middorsal marks or chevrons on the back. One individual (MNRJ 37940) has an occipital spot and an X-shaped mark on the middorsum. Brown markings on the head consist of as many as three labial bars on a side, and a narrow brown postorbital stripe. There is no canthal stripe. Narrow transverse dark brown bars are present on the limbs: two on the forearms, and three each on the thighs, shanks, and tarsi. The flanks and posterior surfaces of the thighs are tan; the venter is uniformly cream, with small brown spots.

COLOR IN LIFE

No thorough description is available. Caramaschi and Rodrigues (2007:12 and their Fig. 4) stated that in life, "during the night the color pattern fades to an uniform clear brown color." Examination of color images of four individuals from Estado de Bahia, Brazil—MNRJ 40253 from Mascote; MZUESC 8120, from Serra Bonita; MZUESC 8650 from Reserva Ecológia de Michelin, Ituberá; and MZUESC 9583 from Floresta Azul, Ilhéus—form the basis for the following description, and three of the four are depicted herein (Fig. 10.8). The dorsum is reddish brown, with or without tan blotches. Markings on the head consist of a faint irregular reddish-brown interocular bar, and faint brown labial bars. There are no evident postorbital or canthal stripes. Faint brown transverse bars are present on the dorsal surfaces of the limbs. The posterior surfaces of the thighs, inner surfaces of the shanks, and webbing on the feet are red. The flanks are colored like the dorsum; the venter is cream. The iris is creamy yellow, with reddish-brown reticulations.

MEASUREMENTS

Females are slightly larger than males (Table 10.3) and differ proportionately only in having slightly shorter feet; the mean foot length is 41.5% of the snout–vent length in two females, and 45.8% in three males. A juvenile has a snout–vent length of 21.5 mm.

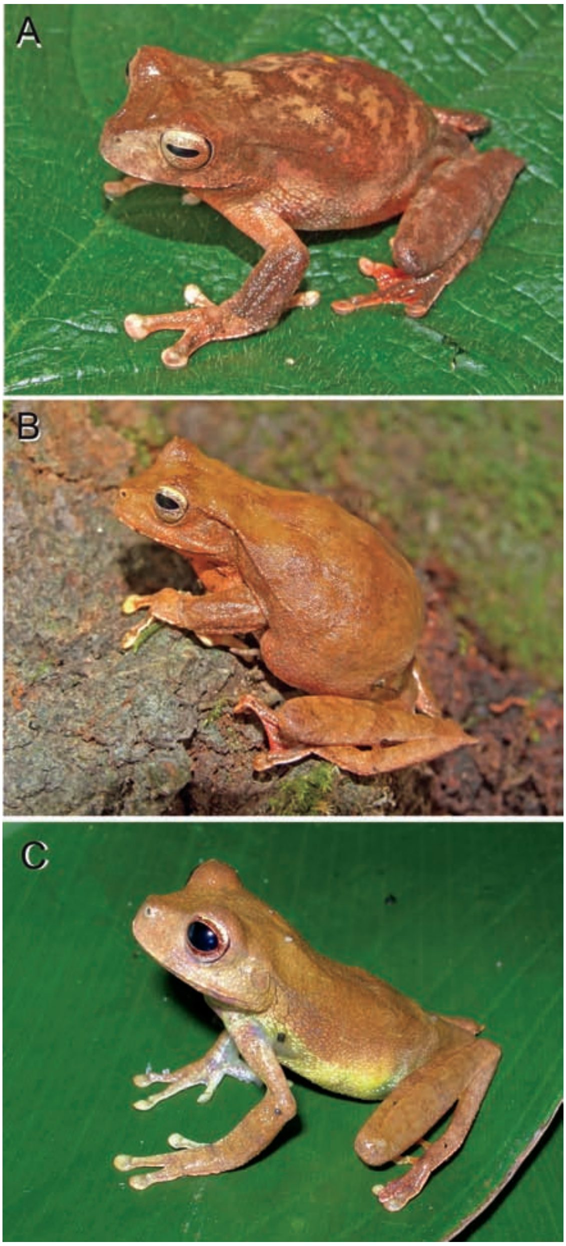

Fig. 10.8 Females of *Gastrotheca pulchra*. A: Floresta Azul, Bahia, Brazil. B: Serra Bonita, Bahia, Brazil. C: MNRJ 40253, 34.2 mm SVL, Fazenda São José, Mascota, Bahia, Brazil. Photos by I. Ribeiro Dias (A and B) and B. Pimenta (C), KUDA.

CRANIAL OSTEOLOGY

Nothing is known.

Life History

One female, having a snout–vent length of 32.6 mm, contained 10 eggs that were each 4.6 mm in diameter in the pouch. The sizes and number of eggs indicate that they hatch as froglets.

Distribution and Ecology

This species inhabits isolated patches of tropical rainforest from eastern Pernambuco to southern Bahia, Brazil (Fig. 10.9).

Conservation Status

In the IUCN Red List, *Gastrotheca pulchra* is categorized as Data Deficient.

Etymology

According to Caramaschi and Rodrigues (2007:12), "the specific epithet *pulchra* is a Latin adjective meaning beautiful, referring to the pretty, tiny, and elegant appearance of this species."

Remarks

Since this species was described in 2007, numerous range extensions (Dos Santos and Dos Santos, 2009; Freitas et al., 2009; C. V. de Mira Mendes, pers. comm.) reflect the activity of many Brazilian biologists who are rapidly increasing our knowledge of the Brazilian herpetofauna.

Gastrotheca (*Eotheca*) *recava* Teixeira, Vechio, Recoder, Carnaval, Strangas, Damasceno, Sena, and Rodrigues

Gastrotheca recava Teixeira, Vechio, Recoder, Carnaval, Strangas, Damasceno, Sena, and Rodrigues, 2012:12.—Holotype: MZUSP 147033 from Estação Ecológica Estadual de Wenceslau Guiamarães, Estado do Bahia, Brazil.

Diagnosis

Adults of this species attain a maximum snout–vent length of 84.9 mm. The tibia length is about 50% of the snout–vent length, and is much shorter than the foot. The interorbital distance is noticeably wider than the upper eyelid. The skin on the dorsum is shagreen, co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is much longer than the second. The discs are nearly twice the width of the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing is basal between the fourth and fifth toes. The dorsum is tan, with brown chevrons. Markings on the head consist of a dark brown subpostorbital stripe and narrow white labial stripe, both of which extend onto

Table 10.3 Univariate statistics for adults of *Gastrotheca pulchra*

	Males ($n = 3$)			Females ($n = 2$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length**	28.3	27.6–29.0	0.70	33.4	32.6–34.2	1.13
Tibia length**	16.0	15.4–16.5	0.55	19.5	19.0–19.9	0.64
Foot length**	13.0	12.8–13.1	0.15	13.9	13.8–14.0	0.14
Head length**	9.2	8.7–9.6	0.45	12.2	12.0–12.3	0.21
Head width**	10.8	10.7–10.8	0.06	13.0	13.0	0.00
Interorbital distance**	3.4	3.2–3.6	0.21	4.1	3.5–4.6	0.78
Eyelid width	3.2	2.9–3.5	0.31	3.7	3.5–3.9	0.28
Internarial distance	2.3	2.0–2.6	0.30	2.3	2.2–2.4	0.14
Eye diameter	3.8	3.4–4.2	0.40	3.8	3.8	0.00
Eye–nostril distance	3.3	3.2–3.5	0.15	3.9	3.6–4.2	0.42
Orbit–jaw distance	2.1	2.0–2.1	0.06	2.2	2.2	0.00
Nostril–jaw distance	3.2	3.2–3.3	0.06	3.3	3.3	0.00
Tympanum diameter	2.2	2.0–2.5	0.25	2.3	2.2–2.4	0.14
Thumb length**	6.2	6.1–6.2	0.06	7.1	7.0–7.2	0.14
Third finger length	9.8	9.6–10.0	0.21	10.4	10.3–10.5	0.14
Disc length	1.7	1.7–1.8	0.06	1.8	1.7–1.9	0.14

**Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

the flank. A pale dorsolateral stripe is absent. The belly is cream.

Four species of *Gastrotheca* in northeastern Brazil differ from all other members of the genus by having broad heads, with the roofing bones of the skull co-ossified with the overlying skin. Among these species, *G. recava* is unique in lacking a distinct suborbital brown bar, and in having a white labial stripe that extends onto the flank. The posterior border of the skull is approximately straight in *G. megacephala* and *G. prasina*, in contrast to the scalloped or indented margins in *G. fissipes* and *G. recava*; furthermore, *G. fissipes* can be distinguished from *G. recava* by having a broad suborbital bar that is not continuous with the postorbital stripe. Two other species, *G. flamma* and *G. pulchra*, differ from *G. recava* by having calcars on the heels and tubercles of the margin of the upper eyelids.

Description

The following description is based on six adults, plus information from the original description by Teixeira et al. (2012). The body is robust; males of this large species attain a snout–vent length of 75.4 mm, and 84.9 mm in females. The snout is narrowly truncate terminally, but is acutely rounded in general shape, and is high and truncate in profile. The canthus rostralis is acutely angular in cross-section. The loreal region is concave; the lips are narrowly rounded. The top of the head is flat. The interorbital distance is slightly wider than the upper eyelid. The internarial area is slightly depressed. The nostrils are barely protruding, and are directed laterally at a point below the anterior terminus of canthus rostralis slightly posterior to the anterior margin of the lower jaw. The diameter of the eye is slightly greater than its distance from the nostril. The tympanum is broadly elliptical in a vertical axis, and is separated from the eye by a distance greater than the length of the tympanum. The tympanic annulus is distinct and smooth. A bony supratympanic crest extends in an anterior-posteroventral plane to the level of the posterior edge of the tympanum. An elevated transverse occipital crest is absent.

The arm is moderately slender, and lacks ulnar tubercles. The hand is large. The fingers are moderately long and unwebbed. The fingers have large round discs; the width of the disc on the third finger is less than the length of the tympanum. Finger I is much longer than Finger II. The relative lengths of the fingers are I > II < IV < III. The subarticular tubercles are small and subconical; supernumerary tubercles are absent. The palmar tubercle is prominent and ovoid; the prepollical tubercle is elongate; in breeding males the median edge of the prepollical tubercle bears a brown nuptial excrescence. The hind limb is moderately slender. The tibia length is less than 55% of the snout–vent length; the foot length is less than 40% of the snout–vent length. A calcar and tarsal fold are absent. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is ovoid, and is visible from above. The toes are moderately long. The relative lengths of the toes are

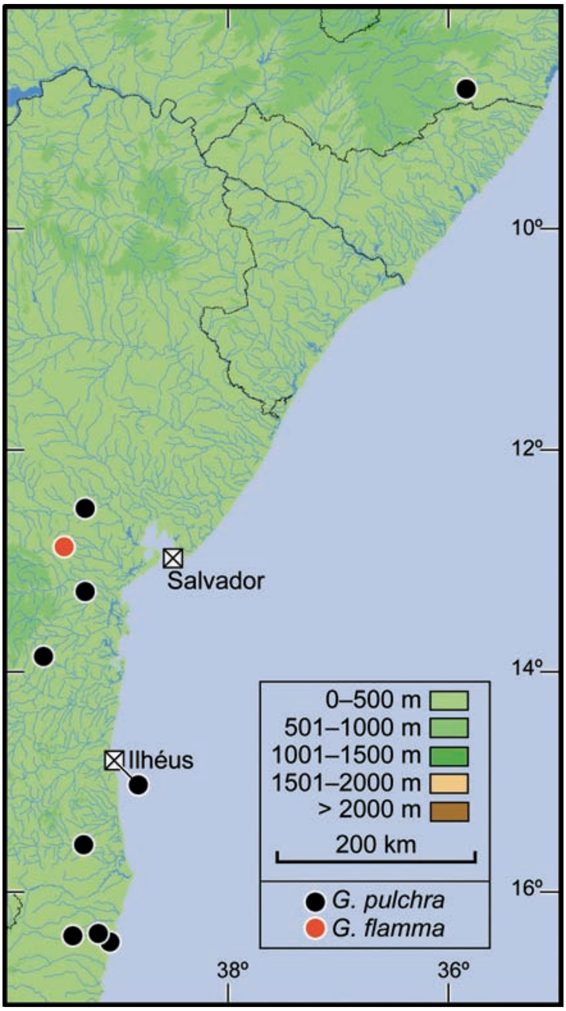

Fig. 10.9 Eastern Brazil, showing the localities of known occurrences of *Gastrotheca flamma* and *G. pulchra*.

I < II < III < V < IV. The inner toes are not webbed; the outer toes are webbed basally. The subarticular tubercles are small and subconical; supernumerary tubercles are present on the proximal segments.

The skin on dorsum is shagreen; all skin on the head (except the eyelids) is co-ossified with the underlying cranial elements; the dorsal surfaces of the hind limbs and flanks are smooth; the belly and posteroventral surfaces of the thighs are granular; the other ventral surfaces are smooth. A pair of subconical tubercles is present ventrolateral to the cloacal opening. The pouch opening is broadly V-shaped, with the anterior margin at the level of the posterior edge of sacrum. The dentigerous processes of the vomers are posteromedially inclined, and are widely separated medially between the large ovoid choanae. Each process bears five to six teeth.

COLOR IN PRESERVATIVE

The dorsal surfaces of the head and body are tan to dull brown. Most individuals have a narrow interorbital bar that originates on the eyelids. Dorsal markings, when present, consist of two darker brown chevrons. The limbs are tan, with dark brown transverse bars: three on the forearm, four or five on the thigh, and three on the shank. A broad dark brown mark begins below the eye, broadens behind the eye, and extends to midflank. A narrow white labial stripe is continuous with a broader white stripe on the flanks. A pale dorsolateral stripe is absent. The posterior part of the flank, the groin, and hidden surfaces of the thighs are tan, with black reticulations. The ventral surfaces of the belly and hind limbs are dull tan, with or without irregular grayish-brown spots. The subcloacal region is dark brown, with prominent white tubercles.

COLOR IN LIFE

The dorsal surfaces of the head, body, and limbs are tan, with reddish-brown markings; a narrow interorbital bar, continuous or fragmented chevron-shaped marks, and transverse bars are present on the limbs (Fig. 10.10). Markings on the head consist of a narrow brown canthal stripe that continues on the outer edge of the eyelid to a broad brown subpostorbital stripe that extends onto the flank. The brown mark is bordered below by the posterior extension of the labial stripe. The loreal region is green in some individuals. The hidden surfaces of the thighs are cream, with dark brown or black reticulations. The throat and chest are cream, with or without dark brown spots or reticulations. The ventral surfaces of the hind limbs are dark

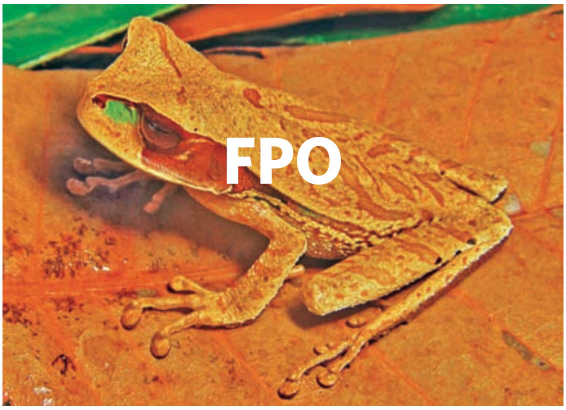

Fig. 10.10 *Gastrotheca recava* (MZUSP), male, Estação Ecológica Estadual de Wenceslau Guiamarães, Bahia, Brazil. Photo by M. Teixeira Jr., KUDA.

gray, with pale mottling. The subcloacal region is brown, with white tubercles. The iris is dark reddish brown.

MEASUREMENTS

The snout–vent length in females is about 10 mm greater than that length in males (Table 10.2).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous fine pit-and-ridge pattern. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange, and has an otic flange that is complete to the squamosal to form a complete temporal arcade. The specimen examined is a tomograph; thus it is not possible to discern some details with certainty. Because the frontoparietal covers the anterior epiotic eminence and the anterior part of the posterior epiotic eminence, it may be fused to them; the condition of the carotid canal is unknown. The alary processes of the premaxillae are nearly vertical (i.e., ≤ 10°); the premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for only about 25% of the length of the rostrum. The pars facialis of the maxilla is distinctly separated from the alary process of the premaxilla, and has only a narrow overlap with the dental process of the premaxilla. The quadratojugal is short. The postorbital process of the maxilla is massive, and has a broad horizontal articulation with the wide zygomatic process of the squamosal. The head of the squamosal bears a wide crest; the otic plate marginally articulates with the crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in size, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has a blunt terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are moderately separated medially, and bear ventral flanges. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a distinct long blunt-tipped dorsal ramus on its anterior arm. The vomers bear moderately large dentigerous processes located between the anterior quadrants of the choanae.

Life History

This species undergoes direct development. One female gave birth to 20 young (Teixeira et al., 2012).

Advertisement Call

Teixeira et al. (2012) reported that the call consists of a single note, 102–115 milliseconds ($\bar{x} = 106$) in length; the notes consist of 2–4 pulses ($\bar{x} = 3.17$), with a dominant frequency of 1102–1630 Hz ($\bar{x} = 1391$). According to these authors, the call reported by Mendes et al. (2012) as that of *Gastrotheca fissipes* actually is the call of *G. recava*.

Distribution and Ecology

Gastrotheca recava is known from several localities in the Atlantic Coastal Forest in northern Bahia, Brazil (Fig. 10.7). According to Teixeira et al. (2012), the species occurs in second-growth forest as well as primary forest. Frogs perching from 10 cm to more than 5 m above the ground were observed on branches of shrubs and trees. Males begin calling shortly before dusk and continue calling throughout the night. At the type locality, two other species of *Gastrotheca* were found: *G. megacephala* and *G. pulchra*.

Conservation Status

It is noteworthy that this newly discovered species has a moderately extensive range that includes protected areas. But because so much of the Atlantic Coastal Forest has been disturbed, *Gastrotheca recava* probably should be categorized as Vulnerable on the IUCN Red List.

Etymology

According to Teixeira et al. (2012), the specific epithet is a Latin adjective, *recavus*, meaning "arched inward" or "concave." The name was used in reference to the posterior edges of the cranial bones, which are arched inward.

Remarks

In contrast to the Bayesian tree provided by Teixeira et al. (2012), showing *Gastrotheca fissipes* to be the basal taxon to the other casque-headed species on northeastern Brazil, the tree presented here has *G. recava* as the sister taxon to the other species (*G. fissipes*, *megacephala*, and *prasina*).

Subgenus *Cryptotheca*, new subgenus

Cryptotheca Duellman. Type species—*Gastrotheca walkeri* Duellman, 1980, by original designation.

Definition
These moderately large frogs bear calcars on the heels. The length of the tibia is 55%–60% of the snout–vent length. The head is moderately large; the mean ratio of head length to snout–vent length is 34.5%, and head length to head width is 37.7%. Females of the species in this subgenus have an elongated V-shaped opening to the brood pouches, which are divided into a pair of lateral pouches that penetrate the body wall and enter into the coelomic cavity.

Osteologically, *Cryptotheca* is characterized by a suite of plesiomorphic features that resemble those of its basal sister taxon *Stefania* and distinguish it from the heavily casqued members of *Eotheca*. The skin of the skull does not adhere to the underlying roofing bones, which are exostosed in a coarse pattern of dermal sculpturing, except for the sphenethmoid, which is smooth. The roofing bones of the skull have incomplete medial articulations and a minimal development of the flanges. The zygomatic ramus of the squamosal does not articulate with the maxilla, and the pterygoid lacks any articulation with the squamosal.

Reproduction
The eggs undergo direct development and emerge as froglets.

Distribution
This subgenus inhabits cloud forest at elevations of 650–1340 m in the Cordillera de la Costa and the Sierra de Aroa in northern Venezuela. Possibly it also occurs on the adjacent Caribbean lowlands (*Cryptotheca williamsoni*).

Content
Two species.

Etymology
The name is derived from the Greek *krypto*, meaning "concealed," and the Greek *thekes*, meaning "containers." The name is used in reference to the pair of retroperitoneal brood pouches in these frogs.

Remarks
In the Bayesian analysis of two nuclear and three mitochondrial genes by Wiens et al. (2007), *Gastrotheca walkeri* was placed as the sister taxon to the group of species now placed in the subgenus *Amphignathodon*; the same arrangement was obtained in a maximum likelihood analysis by Blackburn and Duellman (2013) and in the analysis presented here (chapter 3). The lateral retroperitoneal brood pouches are unique to this subgenus.

KEY TO SPECIES OF *CRYPTOTHECA*

1. Fingers about one-fourth webbed; Finger I longer than Finger II; triangular supraciliary process .... *G. walker*
2. Fingers about one-half webbed; Fingers I and II equal in length; no supraciliary process.................... *G. williamsoni*

Gastrotheca (*Cryptotheca*) *walkeri* Duellman

Gastrotheca walkeri Duellman, 1980:1.—Holotype: UMMZ 117177 from between the Estación Biologica Rancho Grande and Paso Portachuelo, 1100 m, Estado de Aragua, Venezuela.
Gastrotheca (*Opisthodelphys*) *walkeri*—Dubois, 1987:31.

Diagnosis
This is a moderately large species that attains a maximum snout–vent length of 70.6 mm. The tibia length is less than 60% of the snout–vent length, and is much longer than the foot. The interorbital distance is only slightly greater than the width of the upper eyelid. The skin on the dorsum is smooth, with scattered granules; it is not co-ossified with the skull, lacks transverse ridges, but has a granular interocular ridge. The supraciliary processes are small and triangular. The heel bears a small triangular calcar. The tympanic annulus is granular. The first finger is longer than the second. The discs on the fingers are much wider than the digits proximal to the discs. The fingers are about one-fourth webbed; on the foot the webbing extends maximally to the distal subarticular tubercles on the fourth and fifth toes. The dorsum is tan, with darker narrow chevrons. Markings on the head consist of a dark canthal stripe and interocular bar, and a pale suborbital bar. A pale dorsolateral stripe is absent. The flanks are tan, with brown diagonal marks; the venter is cream.

Gastrotheca walkeri is most similar to *G. williamsoni*, which differs by having the fingers about one-half webbed, the first and second fingers equal in length, and a smooth tympanic annulus, as well as by lacking supraciliary processes. In addition to *G. walkeri* and *G. williamsoni*, three other species of *Gastrotheca* (*G. andaquiensis*, *cornuta*, and *dendronastes*) have a granular interocular ridge; the last two also have transverse ridges on the body. *G. andaquiensis* has larger supraciliary processes; first and second fingers equal in length; a green or brown dorsum, with darker mottling; and uniformly dark flanks.

Description

The following description is based on 19 specimens. The body is moderately robust; the maximum snout–vent length is 70.6 mm in females, and the largest male is a subadult with a snout–vent length of 47.3 mm. The head is casqued, but not co-ossified. The head is slightly wider than long, but not as wide as the body. The snout is rounded in dorsal view, and in profile is inclined anteroventrally from the nostrils to its tip. The canthus rostralis is angular in cross-section. The loreal region is concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 130% of the width of the upper eyelid. The internarial area is flat. The nostrils are not protuberant, and are directed anterolaterally at the terminus of the canthus rostralis at a point just posterior to the anterior margin of the lower law. The diameter of the eye is about equal to its distance from the nostril. The tympanum is round, and is separated from the eye by a distance nearly twice the length of the tympanum. The tympanic annulus is indistinct and granular. The supratympanic fold is weak, barely obscures the upper edge of the tympanum, and extends onto the flank to about midlength of the body.

The arm is moderately robust, and bears a row of conical ulnar tubercles. The hand is moderate in size. The fingers are moderately long, and bear large round discs; the width of the disc on the third finger is slightly greater than the length of the tympanum. The relative lengths of the fingers are I > II < IV < III. The fingers are about one-fourth webbed; the webbing formula is **II**(2–2^+)—(3–3^+)**III**(2½–3^-)—(1½–2^+)**IV**. The subarticular tubercles are large and round, and none are bifid; the supernumerary tubercles are moderately large, round, and present only on the proximal segments. The palmar tubercle is low, diffuse, and bifid. The prepollical tubercle is elliptical; nuptial excrescences are not evident. The hind limb is moderately slender. The tibia length is about 58% of the snout–vent length; the foot length is about 44% of the snout–vent length. The heel bears a small triangular calcar. Tarsal tubercles and an outer metatarsal tubercle are absent; the inner tarsal fold is low, and is weak on the distal one-fourth of the tarsus. The inner metatarsal tubercle is elliptical, and is barely visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. The toes are about four-fifths webbed; the webbing formula is **I**(1–1^+)—(2^-–2^+)**II**1—(2^-–2^+)**III**1—(1^+–2)**IV**(1^+–2)—1**V**. The subarticular tubercles are large and round; the supernumerary tubercles are small, diffuse, and present only on the proximal segments.

The skin on the dorsum is smooth, with scattered small granules. The skin on the flanks is areolate; the skin on the belly and ventral surfaces of the thighs is coarsely granular; the skin on the throat is weakly granular. A transverse row of larger granules is continuous between the small triangular supraciliary processes on the margins of the upper eyelids. Small tubercles are present in the tympanic region; the supratympanic-dorsolateral fold is granular. The cloacal opening is bordered below by two pairs of tubercles. The outline of the brood pouches is elongately V-shaped, with its anterior margin at the level of the sacrum; the openings of the pouches are under the lateral folds. The dentigerous processes of the vomers are transverse, and are moderately separated medially between the choanae. Each process bears five to nine teeth.

COLOR IN PRESERVATIVE

The dorsum is tan to reddish brown, with diffuse brown flecks. Its markings consist of an irregular narrow canthal line; a narrow interocular stripe on the transverse row of granules; an indistinct quadrangular blotch in the occipital-scapular region; two curved diagonal bars extending onto the upper parts of the tan flanks; followed posteriorly by one to three chevrons terminating diffusely on the upper flanks, where they form fields of dark flecks. The limbs are colored like the dorsum, with indistinct transverse bars and alternating wide and narrow bars on the hind limbs. The anterior and posterior surfaces of the thighs are uniformly tan, with dark flecks on the posterior surfaces. The outer toes and intervening webbing are a darker brown than the inner toes and webbing. A dark patch is present in the cloacal region; a pale transverse stripe is present above the vent; pale spots usually (84%) are absent below the vent. The tympanic region is brown; the lips are barred with brown; a large pale suborbital bar is present. The venter is dull cream, with (11%) or without (89%) dark flecks.

COLOR IN LIFE

The following color notes are based on specimens from the vicinity of the type locality in Estado de Aragua, Venezuela (Fig. 10.11).

KU 133390–91 from Rancho Grande.—The dorsum varies from a solid dark tan, with slightly darker chevrons and numerous black flecks, to dark brown medially and beige laterally (yellow at night). The limbs are barred. The venter is yellow in the dark tan specimen, and creamy white in the one that has black bars on the flanks. The iris is pale reddish copper, with black reticulations (S. R. Edwards field notes, 7 June 1970).

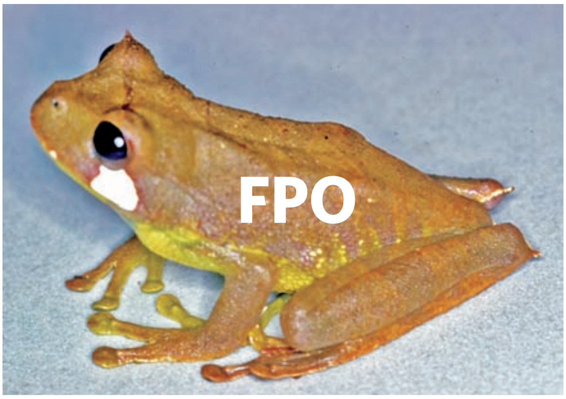

Fig. 10.11 *Gastrotheca walkeri* (KU 166768), female, 53.4 mm SVL, Km 29, Maracay–Ocumare de la Costa road, Aragua, Venezuela. Photo by W. E. Duellman.

KU 166766 from Km 26 on the Maracay–Ocumare de la Costa road.—The dorsal surfaces of the body and limbs are olive green, with sepia-umber markings. White suborbital and post-tympanic bars are present. The flanks are greenish white, with sepia-umber bars. The anterior surfaces of the thighs, upper arms, gular area, ventral surfaces of the limbs, and palmar surfaces are pale green. The belly is cream, with brown flecks and spots. The cloacal and heel stripes are white. The iris is bronze, delicately reticulated with darker brown. The tongue and buccal cavity are green (W. E. Duellman field notes, 3 August 1974).

KU 167851 from KM 26 on the Maracay–Ocumare de la Costa road.—The dorsum is olive tan, with reddish-brown flecks. Distinct dark marks, bars on the flanks and limbs, and white suborbital and post-tympanic bars are absent. There is a faint indication of suborbital bars. The plantar surfaces and webbing are reddish brown. The cloacal and heel stripes are indistinct. The belly lacks brown flecks and spots (W. E. Duellman field notes, 4 August 1974).

MEASUREMENTS

No adult males are available; therefore measurements of adult and subadult females are compared with those of subadult males (Table 10.4).

CRANIAL OSTEOLOGY

The sphenethmoid is smooth and unsculptured, whereas the other bones of the skull table bear coarse pit-and-ridge dermal sculpturing; thus the skull table has a heterogeneous pattern. The nasals do not articulate medially; their borders are distinct from the sphenethmoid. The nasal lacks a posterolateral articulation with the anterolateral margin of the frontoparietal. The frontoparietals have an incomplete articulation medially; each bears a narrow supraorbital flange, but no otic flange. A temporal arcade is absent. The frontoparietal does not cover the epiotic eminences; hence the carotid canal is open and, posteriorly, exits the skull adjacent to the posterior epiotic eminence.

Table 10.4 Univariate statistics for adults and subadults of *Gastrotheca walkeri*. Differences between the means of the sexes for all measurements are significant (ANOVA, $P \leq 0.01$).

	Males ($n = 8$)			Females ($n = 11$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	43.8	40.3–47.3	2.76	60.4	42.4–70.6	8.75†
Tibia length	25.6	22.7–27.4	1.61	34.7	24.8–39.8	4.65†
Foot length	19.4	17.0–21.5	1.63	27.5	19.6–31.7	4.13†
Head length	15.3	13.2–17.2	1.33	21.0	14.8–24.5	2.92†
Head width	16.2	14.5–18.0	1.11	22.8	15.9–26.2	3.17†
Interorbital distance	4.4	3.8–4.8	0.37	6.9	4.4–9.1	1.40†
Eyelid width	3.9	3.2–4.7	0.47	4.7	3.7–5.8	0.69†
Internarial distance	3.2	2.9–3.4	0.19	4.2	2.8–5.0	0.56†
Eye diameter	4.6	3.7–5.1	0.46	5.9	4.4–7.2	0.89†
Eye–nostril distance	4.5	3.9–5.4	0.43	5.9	3.7–7.2	0.99
Orbit–jaw distance	1.8	1.4–2.2	0.29	3.0	1.7–4.0	0.64
Nostril–jaw distance	2.7	2.5–3.0	0.21	4.2	2.6–5.3	0.84†
Tympanum diameter	2.3	1.8–2.6	0.31	3.1	2.1–4.0	0.63†
Thumb length	8.2	7.0–9.2	0.74	11.8	8.3–14.3	1.74
Third finger length	14.3	11.0–16.5	1.72	19.9	14.2–23.1	2.85
Disc width	2.7	2.2–3.4	0.46	3.9	2.6–5.0	0.77

†Variances are non-homogeneous (Brown-Forsythe test, $P \leq 0.05$).

The alary processes of the premaxillae are deflected posteriorly, at an angle between 31° and 45°. The premaxillae lack long spinous medial processes. A notch distinguishes the preorbital process from the facial process of the maxilla, which has a short (< 25%) articulation with the nasal; the pars facialis is distinctly separated from the alary process of the premaxilla, has a substantial overlap with the alary process of the premaxilla, and has only a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The maxilla lacks a distinct postorbital process, as well as an articulation with the slender zygomatic ramus of the squamosal, which extends only about half the distance to the maxilla. The head of the squamosal lacks a crest; the otic plate completely articulates with and moderately overlaps the ossified crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in length, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The ossification of the sphenethmoid terminates in the midlevel of the orbit, where it is separated by cartilage from the prootic. The neopalatines are widely separated medially; the ventral ridge of the neopalatine is smooth. The pterygoid does not articulate with the squamosal, and lacks a dorsal ramus on its anterior ramus. The vomers bear moderately large dentigerous processes located between the anterior quadrants of the choanae.

Life History

The eggs undergo direct development into froglets. One female (snout–vent length 60.3 mm) gave birth to 21 young on 1 September; another female (snout–vent length 55.0 mm) gave birth to 13 young on 13 December. A female (snout–vent length 69.0 mm) collected in August contained 31 ovarian eggs, and one (snout–vent length 65.1 mm) collected in October contained 17 developing young in the pouches. Another female (snout–vent length mm) has 14 young associated with it. Recently born young have snout–vent lengths of about 16 mm.

Advertisement call

No call has been associated with this species.

Distribution and Ecology

Gastrotheca walkeri is known only from elevations of 650–1340 m in the Cordillera de la Costa and the Sierra de Aroa in northern Venezuela (Fig. 10.12). It inhabits moist premontane forest and cloud forest. Most individuals have been found at night, 1–2 m above the ground, on branches of bushes or trees, but two were on a cliff in the spray zone of a waterfall. One adult female emerged from a hole in the ground by day, and a juvenile was found in a bromeliad by day.

Conservation Status

In the IUCN Red List, *Gastrotheca walkeri* is listed as Data Deficient. It does occur in some protected areas.

Etymology

The specific name *walkeri* is a patronym for the late Charles F. Walker, who first recognized this hitherto undescribed species (Duellman, 1980).

Remarks

Gastrotheca walkeri is like *G. williamsoni* in having a pair of retroperitoneal brood pouches. The opening of the pouch is beneath the paravertebral folds posterior to the sacrum; each pouch extends ventrolaterally between the skin and the body wall to a point on the flank, where it passes through a large hiatus in the body

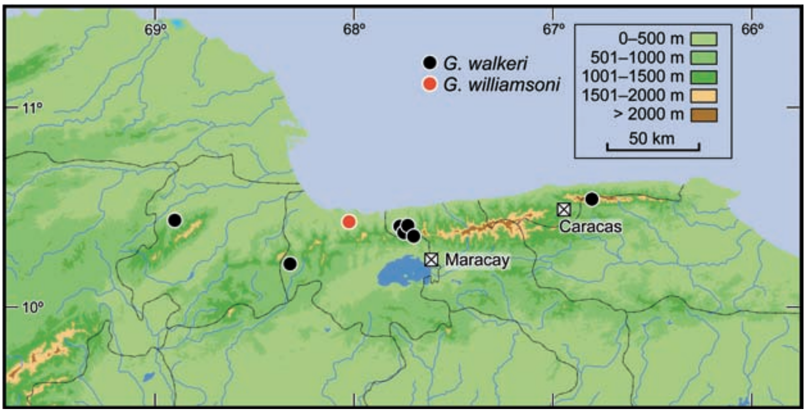

Fig. 10.12 Northern Venezuela, showing the localities of known occurrences of *Gastrotheca walkeri* and *G. williamsoni*.

wall. The thin-walled pouch is barely evident when not filled with developing eggs; when filled, the distended pouches occupy a large proportion of the posterior part of the coelomic cavity.

Gastrotheca (*Cryptotheca*) *williamsoni* Gaige

Gastrotheca williamsoni Gaige, 1922:1.—Holotype: UMMZ 55559 from San Esteban, Estado de Carabobo, Venezuela.
Gastrotheca (*Opisthodelphys*) *williamsoni*—Dubois, 1987:31.

Diagnosis

This medium-sized species has a maximum known snout–vent length of 53.8 mm. The tibia length is less than 55% of the snout–vent length, and is longer than the foot. The interorbital distance is noticeably greater than the width of the upper eyelid. The skin on the dorsum is smooth, not co-ossified with the skull, and has a granular interocular ridge. Supraciliary processes are absent. The heel bears a triangular calcar. The tympanic annulus is smooth. The first and second fingers are equal in length; the fingers have discs that are much wider than the digits proximal to the discs. The fingers are about one-half webbed; on the foot the webbing extends maximally to the distal subarticular tubercle on the fourth and fifth toes. The dorsum is pale, with a darker middorsal blotch anteriorly and chevrons posteriorly. Markings on the head consist of a dark canthal stripe and interocular bar, and a pale suborbital spot. A pale dorsolateral stripe is absent. The flanks are uniformly pale; the venter is uniformly cream.

Gastrotheca williamsoni most closely resembles *G. walkeri*, which differs by having supraciliary processes, the first finger longer than the second, a granular tympanic annulus, and fingers that are only about one-fourth webbed. In addition to *G. williamsoni* and *G. walkeri*, three other species (*G. andaquiensis*, *cornuta*, and *dendronastes*) have granular interocular ridges; the latter two species also have transverse ridges on the dorsum. *G. andaquiensis* differs from *G. williamsoni* by having supraciliary processes; a granular tympanic annulus; a green or brown dorsum, with darker mottling; and uniformly dark flanks.

Description

The following description is based on one specimen, the holotype. The body is robust; the snout–vent length in the single female is 53.8 mm. The head is slightly wider than long, but not as wide as the body. The snout is bluntly rounded in dorsal view, rounded above, and inclined to the tip in profile. The canthus rostralis is rounded in cross-section. The loreal region is slightly concave; the lips are rounded. The top of the head is flat. The interorbital distance is 160% of the width of the upper eyelid. The internarial area is flat. The nostrils are not protuberant, and are directed anterodorsally at the terminus of the canthus rostralis at a point just posterior to the anterior margin of the lower lip. The diameter of the eye is 78% of its distance from the nostril. The tympanum is vertically ovoid, and separated from the eye by a distance slightly greater than the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately heavy, and extends from the posterior corner of the orbit to a point above the axilla; the fold obscures the upper and posterodorsal edges of the tympanum.

The arm is moderately robust, and lacks ulnar tubercles. The hand is small. The fingers are moderately short, and bear large round discs; the width of the disc on the third finger is slightly less than the length of the tympanum. The relative lengths of the fingers are I < II < IV < III. The fingers are about one-half webbed; the webbing formula is **II**2^{-}—3^{-}**III**2½—1^{-}**IV**. The subarticular tubercles are large and round; none are bifid. The supernumerary tubercles are low and diffuse. The palmar tubercle is bifid; the prepollical tubercle is elliptical. The condition of the nuptial excrescences is unknown. The hind limb is moderately slender. The tibia length is 50.6% of the snout–vent length; the foot length is 39.2% of the snout–vent length. The heel has a large triangular calcar. Tarsal tubercles, a tarsal fold, and an outer metatarsal tubercle are absent. The inner metatarsal tubercle is elliptical, and not visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III = V < IV. The toes are fully webbed; the webbing extends to the base of the disc on each digit. The subarticular tubercles are round; supernumerary tubercles are absent.

The skin on the dorsum is smooth; the skin on the flanks is areolate; the skin on the belly and posteroventral surfaces of the thighs is coarsely granular; the other ventral surfaces are smooth. There is a transverse row of small tubercles between the edges of the upper eyelids; cloacal folds and tubercles are absent. The opening of the brood pouches is in the form of an elongate V, with the anterior margin just posterior to the sacrum. The dentigerous processes of the vomers are transverse and narrowly separated medially at the level of the choanae. Each process bears six teeth.

COLOR IN PRESERVATIVE

According to Gaige's (1922:2–3) description, written when the specimen was two years old: "Color (in alcohol) reddish gray above, obscurely spotted with dark; a darker spot on back just behind head; an angular dark, light-edged mark in front of pouch with the angle directed forward, and another faint angular mark in front of the anus and within pouch opening; under lip with indistinct vertical bars; limbs banded with dark; a row of tiny dark-edged tubercles connecting the eyelids across the interorbital space. Sides light with dark vertical bars which slant slightly forward above; back of thighs dark with small light spots. Throat yellowish white; belly and lower surfaces of limbs grayish yellow." When I first examined the specimen on 30 November 1978, it had faded to a pale grayish tan, with faint brown markings consisting of a canthal stripe, narrow interocular bar interrupted medially, narrow supratympanic line, short transverse line in the scapular region, and diffuse brown chevron anterior to the pouch opening (Fig. 10.13).

COLOR IN LIFE

The color in life is unknown.

MEASUREMENTS

The female holotype has the following measurements (in mm): snout–vent length 53.8; tibia length 27.2; foot length 21.1; head length 18.0; head width 19.4; interorbital distance 6.4; upper eyelid width 4.0; internarial distance 4.1; eye diameter 5.7; eye–nostril distance 4.5; orbit–jaw distance 3.0; nostril–jaw distance 3.7; tympanum diameter 3.5; thumb length 8.1; third finger length 15.3; and width of disc on third finger 3.0.

CRANIAL OSTEOLOGY

Limited osteological information was obtained from radiographs of the holotype. The dermal roofing bones are not co-ossified with the overlying skin. The sphenethmoid is not sculptured. The nasals do not articulate medially; their borders are distinct from the sphenethmoid. The frontoparietals have an incomplete articulation medially. Each frontoparietal bears a narrow supraorbital flange; an otic flange and temporal arcade are absent. The head of the squamosal has a narrow crest; the zygomatic ramus extends more than halfway to the maxilla. The cultriform process of the parasphenoid terminates posterior to the level of the neopalatines, which are moderately separated medially and form the posterior margins of the choanae. The median ramus of the pterygoid is expanded medially.

Life History

The holotype contains fully developed young in the pouches.

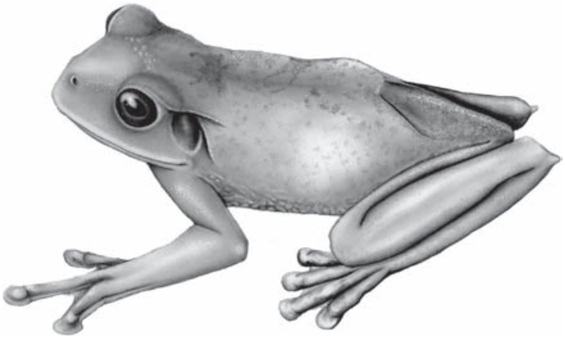

Fig. 10.13 *Gastrotheca williamsoni* (UMMZ 55559, holotype), female, 53.8 mm SVL, San Esteban, Carabobo, Venezuela. Drawing by A. Lathrop.

Advertisement Call

The call is unknown.

Distribution and Ecology

The species is known only from the type locality, in seasonal rainforest on the Caribbean coast of Venezuela (Fig. 10.12).

Conservation Status

This poorly known species is categorized as Data Deficient in the IUCN Red List. It is known from a single specimens collected nearly a century ago.

Etymology

The specific name *williamsoni* is a patronym for E. B. Williamson, the collector of the holotype.

Remarks

Gastrotheca williamsoni is like *G. walkeri* in having paired retroperitoneal brood pouches. Each pouch extends laterally from the lateral fold of the pouch opening, and ventrolaterally for 5.5 mm to the side of the body, where there is a longitudinal opening (4.9 mm) in the body wall.

Subgenus *Amphignathodon* Boulenger

Amphignathodon Boulenger, 1882:450. Type species: *Amphignathodon guentheri* Boulenger, by monotypy.

Definition

The long-legged arboreal species of *Gastrotheca* that inhabit cloud forest and lowland tropical forest in northwestern South America are placed in *Amphignathodon* (Fig. 10.14). Except for members of the subgenus *Eotheca*, these are the largest species of

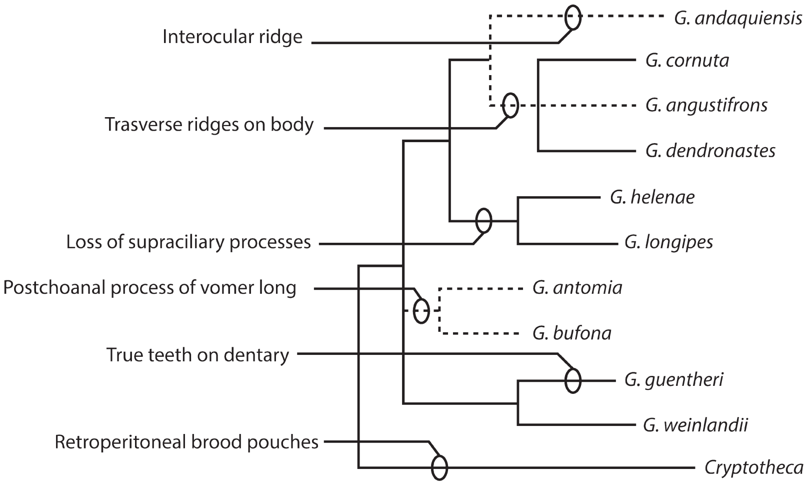

Fig. 10.14 Hypothesized phylogenetic relationships among species of the subgenus *Amphignathodon*, based on molecular data; the tentative placement of species lacking molecular data are shown by dashed lines.

Gastrotheca. Females of *G. angustifrons* attain a known snout–vent length of 91.8 mm, and both sexes of *G. weinlandii* are known to reach a snout–vent length of 86 mm. The smallest species are *G. antomia* and *G. bufona*, neither of which attains a snout–vent length of 70 mm. With the exception of *G. helenae* and some individuals of *G. longipes*, these species are the only members of the entire genus in which the tibia length is greater than 60% of the snout–vent length. Also, these frogs have broad heads; the mean percentage of head length to snout–vent length is 32.1%–38.7%, whereas the relative percentage of head length to head width is 35.8%–44.2%. Likewise, they have proportionally broad interorbital distances, created by the broad supraorbital flanges on the frontoparietals. The mean ratio of interorbital distance to head width ranges from 23.4% in male *G. antomia* to 32.5% in female *G. longipes*. The width of the upper eyelid usually is less than 80% of the interorbital distance; the ratio is only about 50% in *G. helenae*, whereas it is 90.1% in female *G. angustifrons*.

An analysis of osteological characters of *Amphignathodon* does not support the inclusion of *Gastrotheca andaquiensis* and *G. bufona* in the subgenus. The skull roof (including the sphenethmoid) is sculptured in a pit-and-ridge pattern that varies among species in all members of this subgenus except *G. longipes*, which is less well ossified than its sister taxa and is characterized by smooth surfaces and an internal vermiform pattern of ossification. The carotid canal is open, except in *G. angustifrons* and *G. weinlandii*, in which it is partially closed. The dorsal crest of the squamosal is narrow, except in *G. helenae* and *G. weinlandii*, in which it is wide; the otic plate of the squamosal is well developed in all taxa. The postchoanal process of the vomer is short in all taxa except *G. antomia* and *G. bufona*, in which it is long,

Many members of the subgenus also have distinguishing external morphological features. Most species have supraciliary processes and calcars, features that are shared only with *Cryptotheca* in northern Venezuela and *Gastrotheca* (*Eotheca*) *flamma* in eastern Brazil. Transverse dermal ridges on the dorsum of the body and an interocular ridge are present in some species of *Amphignathodon* but are unknown in other *Gastrotheca*. Likewise, certain cranial features characterize members of this subgenus. All of the species in the subgenus have prominent supraorbital flanges on the frontoparietals, distinct dorsal crests on the squamosals, and open carotid canals (partially closed in *G. helenae*). In addition, the otic ramus of the squamosal articulates with and overlaps the crista parotica (no articulation in *G. helenae*). In all but *G. andaquiensis* and *G. longipes*, the zygomatic rami of the squamosals articulate with the maxillae, and a ventral ridge is present on the neopalatines. Except in *G. andaquiensis*, *cornuta*, and *helenae*, the frontoparietals fully articulate medially. *G. guentheri* is unique among all anurans in having true teeth on the mandible; the tooth-like structures on the mandible of *G. bufona* are odontoids.

Reproduction

Members of the subgenus *Amphignathodon* produce eggs that undergo direct development into froglets (unconfirmed in *Gastrotheca angustifrons* and *G. antomia*). Clutch size varies from as few as 7 eggs in one individual of *G. cornuta* to as many as 23 in another female of the same species. The eggs are large; those

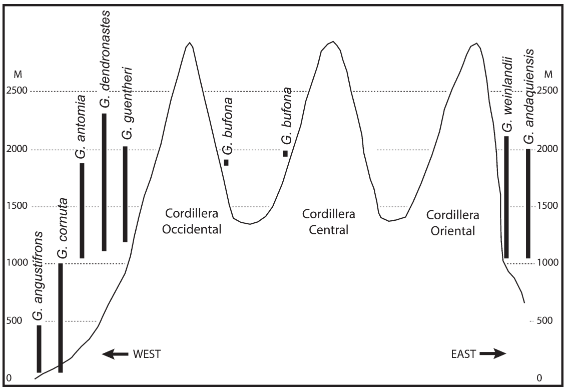

Fig. 10.15 Elevational distributions of members of the subgenus *Amphignathodon* on the Andean slopes in northwestern South America.

being brooded by one female *G. cornuta* were 17 mm in diameter.

Distribution

Except for *Gastrotheca cornuta*, which extends into Central America as far as Costa Rica, the species in the subgenus *Amphignathodon* are distributed on the slopes of the Andes in northwestern South America. Although there is considerable overlap in the elevational distributions of the species, especially on the Pacific versant of the Cordillera Occidental and adjacent Chocoan lowlands (Fig. 10.15), there are few known cases of sympatry. *G. angustifrons* and *G. cornuta* have been reported from lower elevations at Cachabe and Río Cayapas in Provincia de Esmeraldas in northwestern Ecuador, and at Quebrada Ganguí in Departamento de Cauca in southwestern Colombia; *G. cornuta* also occurs sympatrically with *G. dendronastes* at an elevation of 1000 m in the Río Calima Valley in Departamento de Cauca in Colombia. Ruíz-Carranza et al. (1997) commented that *G. antomia* is sympatric with *G. guentheri* at some localities in northwestern Colombia. On the Amazonian slopes of the Cordillera Oriental, *G. andaquiensis* and *G. weinlandii* have been reported from the same two localities: from Cueva de los Guácheros, 2000 m, in Departamento de Huila in Colombia; and from Abitagua, 1100 m, in Provincia de Pastaza in Ecuador. One species, *G. helenae*, occurs in páramo and subpáramo in northeastern Colombia and adjacent Venezuela.

Content

Ten species.

Etymology

The generic name is a combination of three Greek words: *amphi*, meaning “on both sides”; *gnathos*, meaning “jaw”; and *odous*, meaning “tooth.” The name refers to the presence of teeth on both the upper and lower jaws.

Remarks

In the Bayesian analysis of nuclear and mitochondrial genes by Wiens et al. (2007), one major clade with a posterior probability of 0.84 contained six species of *Gastrotheca*. The same arrangement appeared in subsequent phylogenies based on molecular data by Blackburn and Duellman (2013) and Schmid et al. (2013). These six species, together with four species that were not included in the molecular analysis but are similar morphologically, are herein recognized as the subgenus *Amphignathodon*.

Morphometric data for four species in the Chocoan Region (including lower Central America) were subjected to a stepwise discriminant analysis. Significant discrimination was obtained in a four-step model based on head width, interorbital distance, third finger length, and nostril–jaw distance (Fig. 10.16). Of the 70 specimens included in the analysis, 63 (90%) were classified correctly to the a priori categories (species). All *Gastrotheca guentheri* were classified correctly by the variation described on the first canonical axis: head width, interorbital distance, and third finger length. The principal variation described by the second canonical axis involves nostril–jaw distance and distinguishes *G. dendronastes* from *G. angustifrons* and *G. cornuta*. Of the seven specimens classified incorrectly, four are *G. angustifrons* and three are *G. cornuta*.

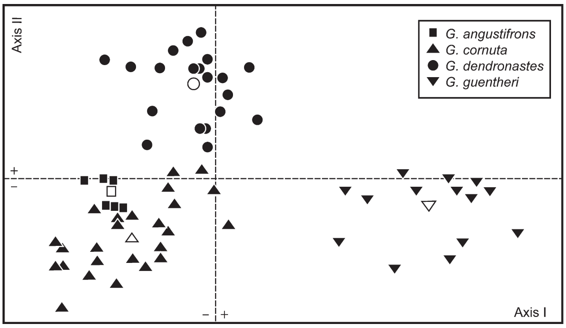

Fig. 10.16 Plot of a multivariate analysis of meristic characters of four species in the *Gastrotheca guentheri* subgroup. Open symbols are the centroids of each species from the cluster analysis.

KEY TO SPECIES OF *AMPHIGNATHODON*

1. Distinct transverse dermal ridges present on dorsum of body 2
   Transverse dermal ridges absent 4

2. Dermal ridges tubercular; interocular ridge present; Finger I longer than Finger II; broad diagonal brown stripe on flank .... *G. dendronastes*
   Dermal ridges smooth; interocular ridge absent; Fingers I and II equal in length; no broad diagonal brown stripe on flank 3

3. Prominent triangular supraciliary processes present .... *G. cornuta*
   Supraciliary processes absent .... *G. angustifrons*

4. Interocular ridge present .... *G. andaquiensis*
   Interocular ridge absent 5

5. Supraciliary processes present; Fingers I and II about equal in length 6
   Supraciliary processes absent 8

6. Heel bearing prominent calcars 7
   Heel having two small tubercles .... *G. antomia*

7. Calcar narrow, elongate, curved; supraciliary process scalloped; inner tarsal fold extending entire length of tarsus .... *G. bufona*
   Calcar broad, triangular; supraciliary process not scalloped; inner tarsal fold absent, replaced by row of tubercles .... *G. guentheri*

8. Finger I much longer than Finger II .... *G. weinlandii*
   Fingers I and II equal in length .... *G. helenae*

Gastrotheca (*Amphignathodon*) *andaquiensis* Ruíz and Hernández

Gastrotheca andaquiensis Ruíz and Hernández, 1976:11.—Holotype: INDERENA 410 from Cueva de los Guácheros, Departamento de Huila, Colombia.

Gastrotheca humbertoi Lutz, 1977:1.—Holotype: formerly in MLS [now lost] from 57 km from "Mocoar" [= Mocoa] on road from that town to Sibundoy, Departamento de Putumayo, Colombia. Synonymy fide Duellman, 1989:106.

Gastrotheca (*Amphignathodon*) *andaquiensis*—Dubois, 1987:31.

Gastrotheca (*Amphignathodon*) *humbertoi*—Dubois, 1987:31

Gastrotheca andaquiensis—Duellman, 1989:106.

Diagnosis

In this large species (females to 76.8 mm), the tibia length is more than 60% of the snout–vent length, and is much longer than the foot. The interorbital distance is slightly greater than the width of the upper eyelid. The skin on the dorsum is finely granular, not adherent to or co-ossified with the skull; a granular interocular ridge and conspicuous supraciliary processes are present. An elongately triangular calcar is present on the heel. The tympanic annulus is granular. The first and second fingers are equal in length. The discs are much wider than the adjacent digits. The fingers are webbed basally; on the foot the webbing extends maximally to the penultimate subarticular tubercle on the fourth toe and the distal subarticular tubercle on the fifth toe. The dorsum is green or tan, with dark green or brown mottling and blotches. Markings on the head consist solely of a pale suborbital bar. A narrow cream dorsolateral stripe is present. The flanks are uniformly dark brown; the venter is uniformly cream.

Of the other species that have supraciliary processes, *Gastrotheca bufona* and *G. guentheri* differ by lacking a granular interocular ridge, by having the skin co-ossified with the skull, and by having different coloration. *G. dendronastes* and *G. walkeri* differ by having the first finger longer than the second, and in coloration. *G. cornuta* differs by having transverse ridges on the dorsum of the body, a shorter calcar, and in coloration.

Description

The following description is based on 15 specimens. The body is robust; the maximum snout–vent length is 62.0 mm in males, and 76.8 mm in females. The head is much wider than long, and as wide as the body. The snout is broadly rounded in dorsal view, deep, and abruptly slopes from the nostrils to the lip in profile. The canthus rostralis is straight, and is rounded in cross-section. The loreal region is slightly concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 115% of the width of the upper eyelid. The internarial area is barely concave. The nostrils are not protuberant, and are directed laterally at a point below the anterior terminus of the canthus rostralis. The diameter of the eye is slightly greater than its distance from the nostril, and is much greater than its distance from the margin of the jaw. The tympanum is vertically ovoid, and is separated from the eye by a distance thrice its length. The tympanic annulus is distinct and tubercular. The supratympanic fold is moderately heavy; it extends from the posterior corner of the eye to a point just posterior to the tympanum, and obscures the upper and posterior edges of tympanum.

The arm is moderately robust; a row of small conical ulnar tubercles is on the outer edge of the forearm. The hand is large. The fingers are long, and are webbed basally; the webbing formula for the outer fingers is **II**2^+—3^+**III**3^-—2½**IV**. The discs are large and round, much wider than width of the digit; the diameter of the disc on the third finger is equal to twice the length of the tympanum. The relative lengths of the fingers are I = II < IV < III. The subarticular tubercles are moderately large, low, and round; supernumerary tubercles are absent. The palmar tubercle is low, bifid, and indistinct; the greatly elongate prepollical tubercle is round in cross-section, and lacks nuptial excrescences. The hind limb is long, and is moderately slender. The tibia length is about 62% of the snout–vent length; the foot length is about 50% of the snout–vent length. The heel bears an elongate triangular calcar; there is a row of low tubercles on the outer edge of the tarsus. Tarsal folds and an outer metatarsal tubercle are absent; the inner metatarsal tubercle is rather small, low, and elliptical. The toes are long. The relative lengths of the toes are I < II < III < V < IV. The toes are about three-fourths webbed; the webbing formula is **I**1—2^- **II**1—2**III**1^-—2**IV**2—1^-**V**. The subarticular tubercles are small, low, and round; the supernumerary tubercles are small, and are present only on the proximal segments.

The skin on the dorsum of the head, body, and limbs is finely granular; the skin on the flanks is deeply areolate; the skin on the belly and posteroventral surfaces of the thighs is coarsely granular; other surfaces are smooth. A distinct granular ridge connects the long pointed supraciliary processes. Cloacal folds and tubercles are absent. The opening of the brood pouch is broadly V-shaped, with the anterior border at the level of the sacrum. The dentigerous processes of the vomers are slightly convex, and are narrowly separated medially between the small round choanae. Each process bears six to nine teeth.

COLOR IN PRESERVATIVE

The dorsum is pale creamy tan to brown, with darker brown markings consisting of indistinct irregular spots and flecks that are extensive and interconnected, so as become dark brown blotches in five specimens. There are narrow transverse bars on the limbs: two or three on each forearm, and three to five on each thigh, shank, and foot. The anterior and posterior surfaces of the thighs are pale tan to cream; the outer two toes and the webbing between them are dark brown; the inner toes and discs on the fingers and toes are cream. Dark brown bands extend from the tympanum to the midflank or groin; the bands are bordered above by narrow cream lines. The side of the head is dark brown, with cream mottling; there is a distinct diagonal bar below the eye in eight specimens. The venter is cream, with a brown suffusion on the posterior part of the belly in three specimens.

COLOR IN LIFE

The dorsal surfaces of the body and limbs usually are green, with brown markings, or brown, with green markings, as shown by the following descriptions of specimens from Colombia and Ecuador.

KU 169420 from 10.3 km W El Pepino, Departamento de Putumayo, Colombia.—The dorsum is avocado green, with dark brown markings (Fig. 10.17A). The upper flanks are dark brown, bordered above by a narrow pale yellow stripe; the lower flanks are cream, with yellow spots. The anterior and posterior surfaces of the thighs and inner surfaces of the hind limbs are green; the cloacal area is dark brown, with a yellowish-tan supracloacal stripe. The outer two toes and webbing between them are dark brown; the other webbing and the discs on the fingers and toes are green. The chin and throat are chartreuse, and the belly and the ventral surfaces of the thighs are creamy yellow. The iris is bright bronze, with brown reticulations; the tongue and the lining of the mouth are bluish green (W. E. Duellman field notes, 28 September 1974).

Four other specimens (KU 169418–19, 169421–22) from the same locality. These differ from KU 169420 by having a brown dorsum, with bright green spots on all dorsal surfaces (Fig. 10.17B); small creamy yellow spots are present suborbitally on the midflank and on the cloacal and ulnar tubercles. The forearms, third and fourth fingers, knees, shanks, tarsi, and fourth and fifth toes are mottled with dark brown; the flanks, axilla, groin, anterior and posterior surfaces of thighs, inner digits, and discs are bright green. A narrow yellow stripe extends from the eye to the flank. The chin and abdomen are chartreuse; the ventral surfaces of the limbs are green. The tongue and buccal lining are bright bluish green (W. E. Duellman field notes, 28–29 September 1974).

Six specimens from 3.5 km W Mera, Provincia de Pastaza, Ecuador.—These are colored like KU 146040. The dorsum is olive green to reddish brown, with indistinct tan spots (Fig. 10.17C); the side of the head and the flanks are dark olive brown. Various pale markings include a pale tan dorsolateral stripe, a cream suborbital bar, and tan webbing. The anterior and posterior surfaces of the thighs are pale orange tan, with or without dull olive-green mottling. The discs, throat, and belly are green, with or without a brown suffusion or brown spots on the posterior part of the

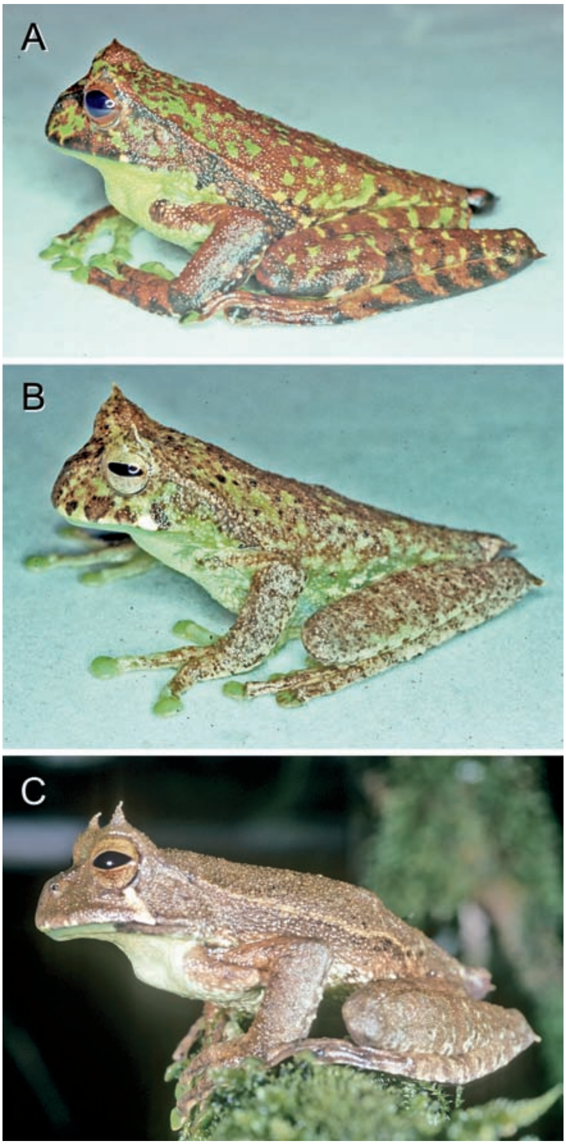

Fig. 10.17 *Gastrotheca andaquiensis*. A: KU 169420, female, 71.7 mm SVL, 10.3 km W El Pepino, Putumayo, Colombia. B: KU 169419, subadult female, 40.8 mm SVL, 10.3 km W El Pepino, Putumayo, Colombia. C: KU 146040, female, 62 mm SVL, 3.5 km W Mera, Pastaza, Ecuador. Photos by W. E. Duellman.

belly; the ventral surfaces of the thighs are dull tan; the tongue and buccal lining are green (W. E. Duellman field notes, 23 April 1972).

Two individuals (unnumbered INDERENA) from Cueva de los Guácheros, Departamento de Huila, Colombia.—Their coloration is greener than that of the others. The dorsum is bright green, with a row of black and white dots on each side of the dorsum; an aqua-blue line traverses the body halfway down the back. The outer edges of the feet are brown; the cloacal region is dark brown, bordered dorsally by pale yellow and below by white spots. The venter is paler green, with white spots along the side; the iris is copper colored (P. E. Gertler field notes, 15 March 1978).

MEASUREMENTS

Females are notably larger than males. An ANOVA of measurements of adults (three males, five females) shows that the means of seven variables are different at $P < 0.01$, and one at $P < 0.05$; all variances are homogeneous (Table 10.5).

CRANIAL OSTEOLOGY

The sphenethmoid is smooth and unsculptured, whereas the other bones of the skull table bear semicoarse pit-and-ridge dermal sculpturing; thus the skull table has a heterogeneous pattern. The nasals do not articulate medially; their borders may or may not be distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a narrow supraorbital flange, but no otic flange. A temporal arcade is absent; although the frontoparietal covers the anterior epiotic eminence, the carotid canal is open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. A notch distinguishes the preorbital process from the facial process of the maxilla, which has a short articulation with the nasal; the pars facialis is distinctly separated from the alary process of the premaxilla, but has a substantial overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The maxilla lacks a distinct postorbital process, as well as an articulation with the slender zygomatic ramus of the squamosal, which extends only about half the distance to the maxilla. The head of the squamosal bears a narrow crest; the otic plate completely articulates with and moderately overlaps the ossified crista parotica. The dorsal part of the stapedial footplate is two to three times the length of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has a blunt terminus posterior to the level of the neopalatines. The sphenethmoid is ossified posterior to the midlength of the orbit, but is not synostosed with the prootic. The neopalatines are moderately separated medially, and do not form the posterior margin of the choanae; the ventral ridge of the neopalatine is smooth. The pterygoid

Table 10.5 Univariate statistics for adults of *Gastrotheca andaquiensis*

	Males ($n = 3$)			Females ($n = 5$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length**	60.0	57.8–62.0	2.11	73.1	65.0–76.8	4.95
Tibia length**	37.6	36.3–39.3	1.54	45.6	43.8–47.5	1.54
Foot length**	30.1	28.7–31.7	1.57	38.1	34.7–41.0	2.36
Head length**	20.0	18.7–21.3	1.30	24.0	22.9–25.0	0.93
Head width**	21.8	20.7–23.0	1.15	26.7	25.1–28.0	1.18
Interorbital distance*	6.9	6.8–7.2	0.23	8.3	7.6–9.5	0.71
Eyelid width	5.5	5.0–6.0	0.50	5.5	5.0–6.0	0.44
Internarial distance	4.2	3.5–4.8	0.66	5.1	4.4–5.8	0.56
Eye diameter	6.3	6.0–6.5	0.25	6.8	6.0–7.8	0.65
Eye–nostril distance*	5.4	5.0–5.7	0.36	6.1	5.7–6.5	0.29
Orbit–jaw distance	3.5	3.2–3.9	0.38	3.8	3.4–4.3	0.33
Nostril–jaw distance	5.1	4.8–5.5	0.35	5.6	4.9–6.1	0.52
Tympanum diameter	3.0	2.4–3.5	0.56	3.0	2.5–3.5	0.46
Thumb length**	12.6	11.6–13.8	1.11	15.9	13.9–16.6	1.16
Third finger length**	21.3	20.2–22.3	1.05	27.1	23.7–29.7	2.22
Disc width	4.3	4.2–4.4	0.10	4.8	4.3–5.3	0.42

*Differences between the means of the sexes are significant (ANOVA, $P = 0.05$).

**Differences between the means of the sexes are significant (ANOVA, $P \le 0.01$).

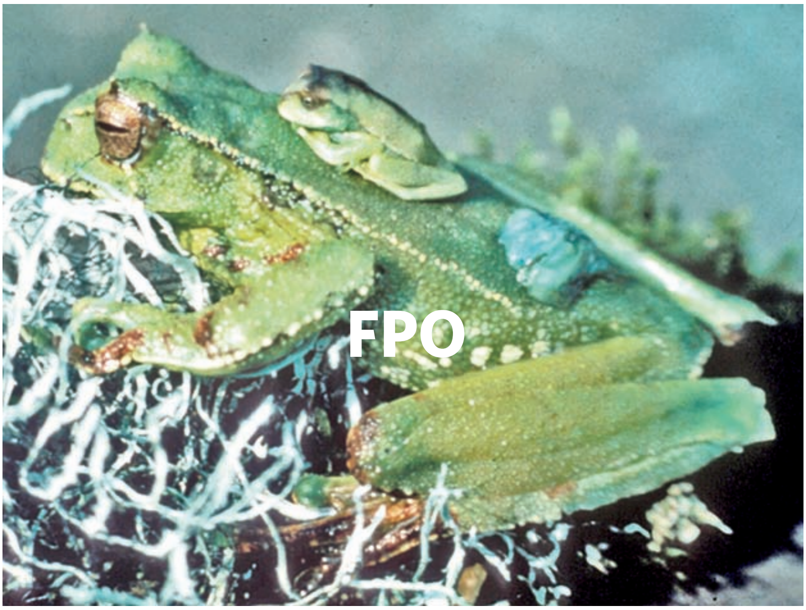

Fig. 10.18 *Gastrotheca andaquiensis* (INDERENA 410), female, 76.0 mm, Cueva de Los Guácheros, Huila, Colombia, with one of 14 newly birthed young on her back. Note the blue lining of the brood pouch. Photo by W. W. Lamar, KUDA.

does not articulate with the squamosal, and lacks a dorsal ramus on its anterior ramus. The vomers bear moderately large dentigerous processes located between the anterior quadrants of the choanae.

Life History

The eggs hatch into froglets. Notes accompanying INDERENA 410 state that the frog was obtained on 15 March 1978, and on the same day it gave birth to 14 young (Fig. 10.18). Six of the young, having snout–vent lengths of 20.7–21.5 mm ($\bar{x} = 21.2$), were preserved with the female, which had a snout–vent length of 76.0 mm. The young have short blunt supraciliary processes, and a short transverse fold on the heel. In life the female was green, with a creamy white dorsolateral line and cream diagonal suborbital bar. All of the newly hatched young were pale green, with a dark gray suffusion middorsally; the side of the head and the dorsolateral stripe were cream. The outer toes of the young were not dark brown, as they are in adults.

Advertisement Call

The call is a loud "wronk," followed by two or three shorter notes, "tonk-tonk." No recordings are available.

Distribution and Ecology

This species is known from localities at elevations of 1100–1935 m on the Amazonian slopes of the Andes of southern Colombia and Ecuador; from an elevation of 1700 m in the Cordillera de Cutucú in southern Ecuador; and from an elevation of 2000 m at Cueva de los Guácheros, on the western slopes of the Cordillera Oriental in the upper Río Magdalena Valley in Colombia (Fig. 10.19).

Two localities (Abitagua and Mera in Ecuador) at elevations of 1100 and 1270 m in the Pastaza Trench are in lower montane rainforest, whereas the other localities are in cloud forest. Most individuals were found at night, 1–2 m above the ground, on branches of bushes and trees adjacent to or overhanging streams. By day two frogs were in bromeliads, one was in a cave, and one was on a leaf in a thicket of *Heliconia*.

Conservation Status

In the IUCN Red List, this species is categorized as Near Threatened, because of its limited range (a statement that is untrue). It does occur in several protected areas on the Amazonian slopes of the Cordillera Oriental in Ecuador.

Etymology

According to Ruíz and Hernández (1976), the specific name *andaquiensis* refers to the Andaqui tribe, whose members inhabit the southern part of the Cordillera Oriental in Colombia.

Remarks

This distinctive species was recognized as an unnamed species by the late Charles F. Walker, who had a specimen (UMMZ 90242) collected by W. C. MacIntyre at Abitagua, Ecuador, in 1939. I obtained a second specimen in 1972. Ruíz and Hernández (1976) were unaware of these specimens and several others that I had collected when they named *G. andaquiensis* on the basis of a single specimen. Subsequently, I was able to compare the holotype and a topotype with material from Ecuador, thereby confirming the conspecificity of these specimens, even though there is much variation in their coloration.

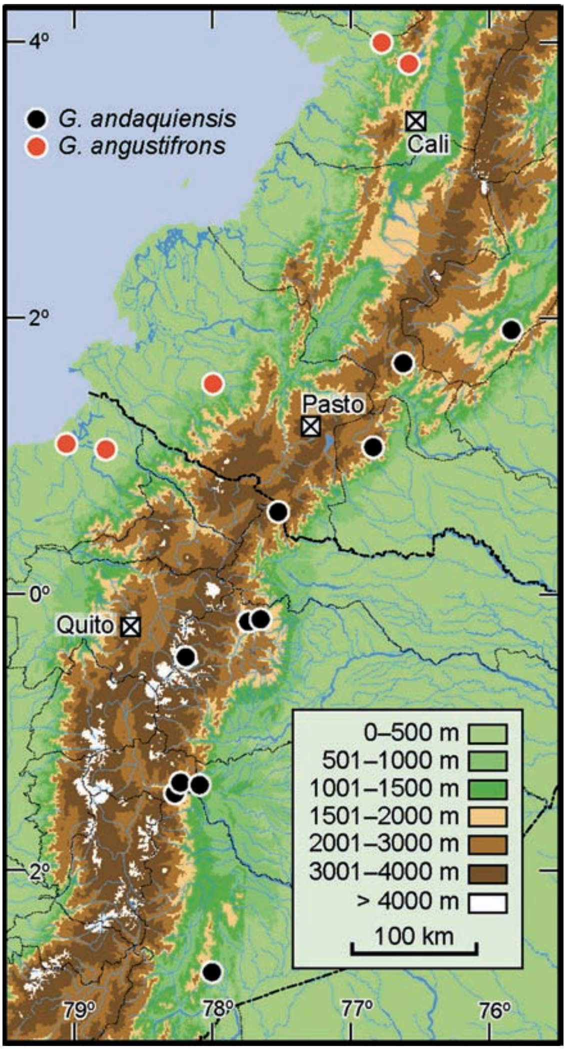

Fig. 10.19 Andean region of Colombia and Ecuador, showing the localities of known occurrences of *Gastrotheca andaquiensis* and *G. angustifrons*.

Lutz's (1977) description of *G. humbertoi* was published after her death. She stated that the sole specimen she had examined, the holotype, was entrusted to her by Hermano Nicéforo María of the Museo de La Salle in Bogotá. The whereabouts of this specimen are unknown. There is no record of it having been returned to the Museo de La Salle; Hermano Daniel Gonzalez and I searched unsuccessfully for the specimen in that collection in March 1979. In October 1978, David C. Cannatella and Antenor Leitão de Carvalho searched unsuccessfully for the specimen among the frogs in the Lutz collection and in the collection in the Museu Nacional in Rio de Janeiro. Along with José Pombal, I also inquired about the specimen in 2011. Thus the holotype (and only assigned specimen) of this nominal species is lost.

The type description of *Gastrotheca humbertoi* is quite detailed; in all characters mentioned, the features of the holotype are essentially in agreement with the characters of *G. andaquiensis*. Consequently, *G. humbertoi* Lutz, 1977, was considered to be a subjective junior synonym of *G. andaquiensis* Ruíz and Hernández, 1976, by Duellman (1989).

Gastrotheca (*Amphignathodon*) *angustifrons* (Boulenger)

Nototrema angustifrons Boulenger, 1898:124.—Syntypes: BMNH 1947.2.22.38–39 from Cachabe, Provincia de Esmeraldas, Ecuador.

Gastrotheca angustifrons—Peters, 1955:339.

Gastrotheca (*Amphignathodon*) *angustifrons*—Dubois, 1987:31.

Diagnosis

In this large species (females to 91.8 mm), the tibia length is more than 60% of the snout–vent length, and is longer than the foot. The interorbital distance is slightly greater than the width of the eyelid. The skin on the dorsum is smooth, not adherent to or co-ossified with the skull, and forms smooth transverse ridges on the body. Supraciliary processes are absent. The heel bears a tubercle. The tympanic annulus is tubercular. The first and second fingers are equal in length. The discs on the fingers are much wider than the adjacent digits. The fingers are webbed basally; on the toes, the webbing extends maximally to the penultimate subarticular tubercle on the fourth toe and the distal subarticular tubercle on the fifth toe. The dorsum is gray or tan, with darker transverse bars. Markings on the head consist of a dark canthal stripe and interocular bar, and a pale suborbital bar; dorsolateral stripes are absent. The flanks are gray, with dark spots; the venter is cream, with dark flecks.

Two other species have transverse dermal ridges on the dorsum: in *Gastrotheca dendronastes* the ridges are tuberculate, whereas they are smooth in *G. cornuta*, which also has a triangular calcar. The heels bear small tubercles in *G. dendronastes*, a species that differs from the others by having longitudinal dark marks on the flanks. Superficially, *G. angustifrons* resembles *G. bufona* and *G. guentheri*, both of which have the skin co-ossified with the underlying dermal bones of the skull.

Description

The following description is based on six adults and one juvenile. The body is moderately robust; the maximum snout–vent length is 73.2 mm in males, and 91.8 mm in females. The head is casqued, not co-ossified, slightly wider than long, and as wide as the body. The snout is rounded in dorsal view and in profile; it barely protrudes beyond the anterior margin of the jaw. The canthus rostralis is straight, and is angular in cross-section. The loreal region is barely concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 115% of the width of the upper eyelid. The internarial area is flat. The nostrils are not protuberant, and are directed laterally at a point below the anterior terminus of the canthus rostralis slightly posterior to the anterior margin of the lower lip. The diameter of the eye is about 15% greater than its distance from the nostril, and is more than twice its distance from the margin of the jaw. The tympanum is nearly round, and is separated from the eye by a distance about 2.5 times the length of the tympanum. The tympanic annulus is tubercular. The supratympanic fold is moderately heavy, extends from the posterior corner of the orbit to a point just posterior to the tympanum, and obscures the upper edge of the tympanum.

The arm is moderately robust; ulnar tubercles are absent. The hand is large. The fingers are long, slender, and webbed basally. The discs are moderately large, round, and much wider than the width of the digit; the diameter of the disc on the third finger is half again the length of the tympanum. The relative lengths of the fingers are I = II < IV < III. The subarticular tubercles are moderately large and round; supernumerary tubercles are absent. The palmar tubercle is indistinct, low, and bifid; the prepollical tubercle is elliptical, and lacks nuptial excrescences. The hind limbs are long and slender. The tibia length is about 65% of the snout–vent length; the foot length is about 51% of the snout–vent length. A small tubercle is present on the heels of four of the six adults; there are no tubercles on the tarsus; an inner tarsal fold is absent. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is small and elliptical. The toes are long and slender. The relative lengths of the toes are I < II < III < V < IV. The toes are about four-fifths webbed; the webbing formula is **I**1—1^{+}**II**1—2^{-}**III**1—(2–2½)**IV**(2–2½)—(1–2)**V**. The subarticular tubercles are moderately small and round; supernumerary tubercles are absent.

The skin on the dorsal surfaces and flanks is smooth. Low smooth transverse dermal ridges are present on the dorsum of the head and body; the anteriormost ridge usually is between the orbits, and extends onto the upper eyelids. A small tubercle is present on the outer edge of the upper eyelid in two specimens. The skin on the throat, belly, and ventral surfaces of the thighs is granular; the other ventral surfaces are smooth. Cloacal decorations are absent. The opening of the brood pouch is narrowly V-shaped, with the anterior border at the level of the sacrum. The dentigerous processes of the vomers are greatly elevated, inclined posteriorly in transverse alignment, and are narrowly separated medially at a level between the small round choanae. Each process bears five to seven teeth.

COLOR IN PRESERVATIVE

The dorsum is tan to pale gray, with faintly darker narrow transverse marks. Three specimens have a dark interorbital bar, canthal stripe, and dorsolateral dark stripe from the eye to midflank. In three specimens the flanks are pale creamy gray, with irregular small dark spots, whereas the flanks in the others are unspotted. The dorsal surfaces of the hind limbs have dark transverse bars: four to six on each thigh and shank, and three to five transverse bars or spots on each tarsus. The posterior surfaces of the thighs are pale gray; the anterior surfaces of the thighs are also pale gray, but with dark bars (three specimens) or spots (four specimens). The side of the head is grayish brown, with a creamy white suborbital spot (absent in one). There is a dark brown patch in the cloacal region, and a pair of cream spots below the cloacal opening. A white transverse supracloacal stripe is present in four specimens. The venter is creamy white, with brownish-gray flecks (absent in one). The outer toes and the webbing are dark brown in four specimens.

COLOR IN LIFE

Specimens from Quebrada Guanguí, Departamento de Cauca, Colombia.—The dorsum is brown, olive brown, or yellowish brown; the venter is white, with or without dark brown markings; a white or pale yellow suborbital bar is conspicuous (Fig. 10.20A). The webbing is brown. The iris is pale bronze brown to pale olive (C. W. Myers field notes, 7 and 17 February 1973).

MEASUREMENTS

Although females reach a larger size than males, no statistical differences were noted in measurements of the small sample examined (Table 10.6).

CRANIAL OSTEOLOGY

The sphenethmoid is smooth and unsculptured, whereas the other bones of the skull table bear semi-coarse pit-and-ridge dermal sculpturing; thus the skull table has a heterogeneous pattern. The nasals do not articulate medially; they articulate with but are not synostosed to the sphenethmoid. The nasal lacks an articulation with the anterolateral margin of the frontoparietal. The frontoparietals lack a complete medial articulation; each bears a narrow supraorbital flange, but no otic flange. A temporal arcade is absent. The frontoparietal completely invests the anterior epiotic eminence; the carotid canal is open and courses over the superficial surface of the frontoparietal. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. A notch distinguishes the preorbital process from the facial process of the maxilla, which has a short articulation with the nasal. The pars facialis is distinctly separated from the alary process of the premaxilla, and has only a narrow overlap with the dental process of the premaxilla.

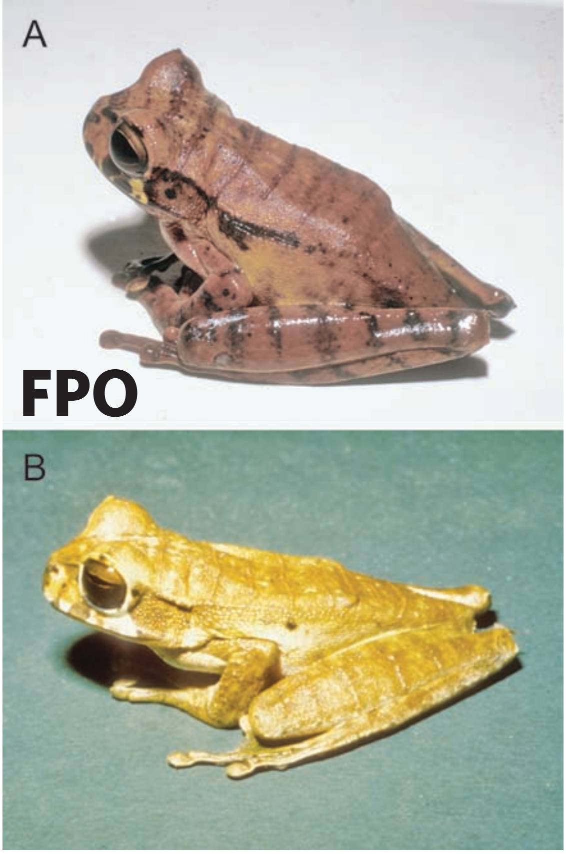

Fig. 10.20 *Gastrotheca angustifrons*. A: AMNH 88200, male, 67.8 mm SVL, Quebrada Guanguí, Cauca, Colombia. B: ICN 13375, male, 69.8 mm SVL, Quebrada Bonita, Valle, Colombia. Photos by C. W. Myers (A) and J. D. Lynch (B), KUDA.

Table 10.6 Univariate statistics for adults of *Gastrotheca angustifrons*

	Males (n = 3)			Females (n = 3)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	65.8	56.5–73.2	8.52	75.8	63.5–91.8	14.52
Tibia length	42.3	36.9–45.2	4.71	50.4	44.4–61.5	9.62
Foot length	34.0	28.2–37.3	5.06	39.5	35.2–48.1	7.42
Head length	22.7	19.5–25.4	2.99	26.5	22.8–31.0	4.16
Head width	24.3	21.9–26.6	2.35	28.0	25.0–32.7	4.14
Interorbital distance	6.9	5.6–7.6	1.10	8.1	6.7–10.8	2.31
Eyelid width	5.8	4.3–6.6	1.27	7.3	4.9–9.6	2.35
Internarial distance	4.2	3.5–4.7	0.64	4.8	4.2–5.4	0.60
Eye diameter	7.2	5.5–8.2	1.50	8.4	6.5–9.7	1.68
Eye–nostril distance	6.2	5.4–6.8	0.74	7.3	6.2–8.5	1.15
Orbit–jaw distance	3.2	2.8–3.6	0.40	4.0	2.9–4.9	1.01
Nostril–jaw distance	5.1	4.3–5.8	0.76	6.3	4.6–7.7	1.56
Tympanum diameter	2.2	1.7–2.6	0.45	2.6	1.9–3.2	0.67
Thumb length	15.2	13.6–16.0	1.72	17.5	15.7–20.1	2.31
Third finger length	24.0	21.3–25.5	2.32	27.5	24.6–31.9	3.87
Disc width	3.8	3.0–4.4	0.71	4.0	3.3–4.8	0.75

The quadratojugal is short. The maxilla lacks a distinct postorbital process, as well as an articulation with the slender zygomatic ramus of the squamosal, which extends only about half the distance to the maxilla. The head of the squamosal bears a narrow crest; the otic plate completely articulates with and moderately overlaps the ossified crista parotica. The dorsal part of the stapedial footplate is slightly larger than the ventral, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has an acuminate terminus. The ossification of the sphenethmoid terminates in the mid-level of the orbit, where it is separated by cartilage from the prootic. The neopalatines are widely separated medially beneath the sphenethmoid, and are smooth ventrally. The pterygoid articulates with the squamosal via a conspicuous spinous dorsal process. The vomers bear moderately large dentigerous processes located between the middle quadrants of the choanae.

Life History

No gravid or brooding females are known. Because all closely related species are known to produce few large eggs that undergo direct development into froglets, *Gastrotheca angustifrons* also is assumed to do so.

Advertisement Call

The call is unknown; presumably it is a loud "bop," like the calls of other long-legged arboreal *Gastrotheca*.

Distribution and Ecology

This species is known definitely from only a few localities, at elevations of less than 200 m in wet tropical forest on the Pacific lowlands of northwestern Ecuador and southwestern Colombia (Fig. 10.19). Two specimens questionably assigned to this species are from elevations of 300 and 460 m in the Río Calima drainage, Departamento de Valle de Cauca, Colombia. All specimens for which field data are available were found on bushes and trees near streams in the forest at night.

Conservations Status

This species is listed as Vulnerable in the IUCN Red List, because of both its fragmented distribution and the destruction of forested habitats on the Pacific lowlands of Colombia and Ecuador. It is not known to occur in any protected area.

Etymology

The specific name is derived from the Latin *angustus*, meaning "narrow," and the Latin *frons*, meaning "forehead."

Remarks

The two specimens from the Río Calima drainage differ somewhat from other specimens of *Gastrotheca angustifrons*. In life, one (ICN 13374) had a pale brown dorsum; the flanks were darker brown, with yellow markings; and the iris was golden brown. The other specimen (ICN 13375) had a brown dorsum, with orange transverse folds; dark brown labial bars and postocular region; pale yellow flanks, with brown reticulations; and a rich brown iris, with a reddish-brown streak (Fig. 10.20B). In both individuals the venter was white, with brown blotches, and the subocular spot was white (J. D. Lynch field notes, 26 and 29 May 1983). Both of these specimens have slightly tuberculate transverse folds on the dorsum; in this regard they resemble *G. dendronastes*, but they differ in having a minute tubercle on the outer edge of each upper eyelid, and a minute tubercle on each heel.

Only minor differences in coloration and morphology exist among the long-legged arboreal species of *Gastrotheca* on the Pacific slopes of Colombia and Ecuador and in lower Central America. Of these four species, *G. guentheri* is the most distinctive, having the unique condition of true teeth on the mandible; furthermore, that species lacks the transverse dermal ridges on the dorsum that are characteristic of the other three species. In order to test for morphometric differences among these four taxa, the morphometric data were subjected to a stepwise discriminant analysis. Significant discrimination was obtained in a four-step model (Fig. 10.16), based on head width, interorbital distance, third finger length, and nostril–jaw distance. Of the 70 specimens included in the analysis, 63 (90%) were classified correctly to the a priori categories (species). All *G. guentheri* were classified correctly by the variation described on the first canonical axis: head width, interorbital distance, and third finger length. The principal variation described by the second canonical axis involves nostril–jaw distance and distinguishes *G. dendronastes* from *G. angustifrons* and *G. cornuta*. Of the seven specimens classified incorrectly, four are *G. angustifrons* and three are *G. cornuta*.

The similarities shown in the discriminant analysis, the presence of two individuals (not included in the discriminant analysis) from the Río Calima drainage that are somewhat like *Gastrotheca cornuta*, and the sympatric occurrence of *G. angustifrons* and *G. cornuta* in northwestern Ecuador and southwestern Colombia all suggest the possibility that *G. angustifrons* is only a variant of *G. cornuta*. Nonetheless, the morphological differences between the taxa are no less than those between some species (e.g., *G. pseustes* and *G. riobambae*) that exhibit distinct molecular differences. Therefore, until new kinds of data dictate otherwise, *G. angustifrons* is considered to be distinct from *G. cornuta*.

Gastrotheca (*Amphignathodon*) *antomia* Ruíz-Carranza, Ardilla-R., Lynch, and Restrepo-T.

Gastrotheca antomia Ruíz-Carranza, Ardilla-R., Lynch, and Restrepo-T., 1997:374.—Holotype: ICN 18331 from Km 21 on the road between Nitibarra and Murri [= La Blanquita], Município de Frontino, Departamento de Antioquia, Colombia.

Diagnosis

In this medium-sized species (females to 58.7 mm in snout–vent length), the tibia length is more than 60% of the snout–vent length, and is longer than the foot. The interorbital distance is much greater than the width of the upper eyelid. The skin on the dorsum is smooth, with scattered conical or subconical tubercles but no transverse ridges; the skin on the top of the head is co-ossified with the underlying cranial elements. Supraciliary processes are present. The heel bears two conical tubercles. The tympanic annulus is smooth. The first finger is shorter than the second. The discs are much wider than the digits. The outer fingers are webbed basally; Toes III–IV are webbed basally. The dorsum is red or brown. Markings on the head consist of diffuse dark brown canthal and postorbital stripes; bars on the upper lips are faint or absent; a dorsolateral stripe is absent. The flanks are brown, with parallel horizontal dark brown stripes; the throat and chest are orange to red; the rest of the venter is black.

Gastrotheca bufona and *G. guentheri* are like *G. antomia* in having long limbs, supraciliary processes, and the skin on the dorsal surfaces of the head co-ossified with the underlying dermal bones of the skull. Both species are larger than *G. antomia*, and are brown or green above and pale brown below. *G. guentheri* also differs from *G. antomia* by having teeth on the dentary, and *G. bufona* differs from *G. antomia* by having only a single tubercle on the heel. In other species having supraciliary processes and calcars (*G. andaquiensis*, *cornuta*, *dendronastes*, and *walkeri*), the skin is not co-ossified with the dermal roofing bones of the skull. Of these, *G. cornuta* and *G. dendronastes* differ by having transverse dermal ridges on the dorsum of the body, and *G. andaquiensis* has a granular interocular ridge; *G. dendronastes* and *G. walkeri* also differ by having the first finger longer than the second, and in coloration.

Description

The following description is based on three specimens. The body is moderately robust; males attain a snout–

vent length of 57.2 mm, and 58.7 mm in females. The head is casqued and co-ossified, noticeably wider than long, and slightly wider than the body. The snout is short, rounded in dorsal view, truncate in profile in females, and inclined anteroventrally from the level of the nostrils to the lip in males. The canthus rostralis is prominent, and is acutely angular in cross-section. The loreal region is concave, and is nearly vertical; the lips are massive and rounded. The top of the head is depressed, owing to dorsal flaring of the lateral margins of the frontoparietals. The interorbital distance is about 165% of the width of the upper eyelid. The internarial region is depressed. The nostrils are protuberant, directed laterally below the anterior terminus of the canthus rostralis at a level slightly posterior to the anterior margin of the lower lip. The diameter of the eye is half again its distance from the nostril, and is nearly twice its distance from the margin of the jaw. The tympanum is small, vertically ovoid, directed posterodorsally, deeply recessed, and separated from the eye by a distance about twice the length of the tympanum. The tympanic annulus is smooth. A supratympanic fold is absent; a serrated dorsolateral ridge of the otic ramus of the squamosal forms a laterally projecting shelf above the tympanum.

The upper arm is slender; the forearm is more robust. A row of small conical ulnar tubercles is present on the ventrolateral edge of the forearm. The hand is large. The fingers are long and slender, with narrow lateral fringes. The fingers are webbed basally. The discs are large and round to subtruncate; the width of the disc on the third finger is half again the width of the digit proximal to the disc, and is twice the length of the tympanum. The relative lengths of the fingers are I < II < IV < III. The subarticular tubercles are large and round; the supernumerary tubercles are large and irregular in shape. The palmar tubercle is large, cordiform, or partially divided into two or three tubercles; the prepollical tubercle is large, ovoid, and about twice as long as wide; nuptial excrescences in males are small and cream or brown. The hind limb is long and slender. The tibia length is about 62% of the snout–vent length; the foot length is about 51% of the snout–vent length. The heel has two prominent conical tubercles; the outer tubercle is much larger than the inner one. A row of conical tubercles is present on the outer edge of the tarsus. A tarsal fold and outer metatarsal tubercle are absent; the inner metatarsal tubercle is small, ovoid, and not visible from above. The toes are long and slender; Toes III–IV are webbed basally. The relative lengths of the toes are I < II < III < V < IV. The subarticular tubercles are round and slightly smaller than those on fingers; the plantar and supernumerary tubercles on the proximal digits are round.

The skin on the head is co-ossified with the underlying cranial elements; the skin on the dorsum of the body is smooth, with scattered conical tubercles; tubercles are especially numerous in the tympanic region. The skin on the belly and posteroventral surfaces of the thighs is coarsely granular; the skin on the throat and chest is finely granular; the other ventral surfaces are smooth. The supraciliary process is elongate and triangular. Conical tubercles are prominent ventral and ventrolateral to the cloacal opening. The opening of brood pouch is broadly V-shaped, with the anterior border at the level of the anterior edges of the sacral diapophyses. The dentigerous processes of the vomers are either moderately long, transverse, and narrowly separated, or are in contact medially at a level behind the large ovoid choanae. Each process bears five to seven teeth. The tongue is cordiform, free behind, and not notched posteriorly. The vocal sac is large, single, median, and subgular; the vocal slits are long and wide, and extend from the midlateral base of the tongue to the angles of the jaws.

COLOR IN PRESERVATIVE

The dorsal surfaces of the head, body, and hind limbs are dark brown; the forelimbs are paler brown. The flanks are pale brown, with or without one or two dark brown horizontal bars. The throat is cream, with brown spots; the belly is dusty brown to dark gray.

COLOR IN LIFE

According to Ruíz-Carranza et al. (1997), all individuals examined by them were homogeneous in coloration in life. The dorsal surfaces of the head, body, throat, and chest are red or purplish or reddish brown (Fig. 10.21); the flanks are brown, with one or two parallel horizontal dark brown stripes; the belly is black. Color photographs show the forelimbs to be brown above, with the median surfaces bright yellow; likewise, the dorsal surfaces of the hind limbs are pale brown, with narrow dark brown transverse bars. The tubercles on the outer edge of the foot and heel are cream. The discs on Fingers I and II and on Toes I–III are orange. The iris is brown, with copper-colored reticulations; the lower eyelid is creamy or bluish green.

MEASUREMENTS

The measurements (in mm) of 16 males are followed by those of 1 female: snout–vent length 32.2–56.9 ($\bar{x}$ =

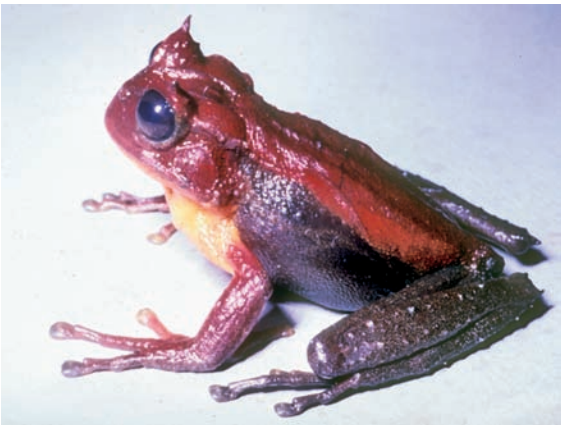

Fig. 10.21 *Gastrotheca antomia*, male, 40.0 mm SVL, Quebrada Canoas, Antioquia, Colombia. Photo by J. D. Lynch, KUDA.

43.0), 57.6; tibia length 20.7–36.7 ($\bar{x}$ = 27.3), 35.4; foot length 18.1–29.9 ($\bar{x}$ = 23.2), 30.3; head length 12.8–20.1 ($\bar{x}$ = 15.8), 29.5; head width 15.3–26.0 ($\bar{x}$ = 19.9), 25.0; interorbital distance, 4.3–8.3 ($\bar{x}$ = 6.0), 8.0; eyelid width 3.3–4.8 ($\bar{x}$ = 4.0), 5.5; internarial distance 2.3–3.9 ($\bar{x}$ = 2.9), 4.0; eye diameter 5.1–6.6 ($\bar{x}$ = 5.8), 6.7; eye–nostril distance 2.8–4.0 ($\bar{x}$ = 3.2), 3.8; orbit–jaw distance 2.2–3.4 ($\bar{x}$ = 2.8), 3.5; nostril–jaw distance 3.2–5.0 ($\bar{x}$ = 3.9), 4.5; thumb length 8.3–12.5 ($\bar{x}$ = 10.4), 13.6; third finger length 13.2–23.4 ($\bar{x}$ = 17.6), 23.0; and width of disc on third finger 2.4–3.5 ($\bar{x}$ = 2.9), 4.5.

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a heterogeneous coarse pit-and-ridge pattern. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange, but lacks a distinct otic flange. A temporal arcade is absent. The frontoparietal covers the anterior epiotic eminence and the anterior part of the posterior epiotic eminence. The frontoparietal is not fused to the epiotic eminence; therefore the carotid canal is open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for about half the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, but has a substantial overlap with the dental process of the premaxilla. The quadratojugal is long. The postorbital process of the maxilla is massive, and has a broad diagonal articulation with the massive zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the otic plate completely articulates with and broadly overlaps the ossified crista parotica. The dorsal part of the stapedial footplate is more than three times the length of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has a blunt terminus between or slightly anterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are moderately separated medially; each bears a low irregular ventral ridge. The pterygoid does not articulate with the squamosal, and lacks a dorsal ramus on its anterior ramus. The vomers bear moderately large dentigerous processes located between the posterior quadrants of the choanae.

Life History

According to Ruíz-Carranza et al. (1997), the eggs undergo direct development into froglets.

Advertisement Call

No data are available.

Distribution and Ecology

Gastrotheca antomia is known only from the western slopes of the Cordillera Occidental in Colombia, where it occurs at elevations of 1140–2500 m from Departamento de Antioquia southward to Departamento de Valle de Cauca (Fig. 10.22). Individuals have been found at night 1.0–2.5 m above the ground, on branches of trees near streams and rivers in cloud forest (Ruíz-Carranza et al., 1997).

Conservation Status

In the IUCN Red List, this species is listed as Vulnerable, because of its limited distribution in forested areas that are being reduced through logging and expanding agriculture. Its range includes the Parque Nacional Natural Tatamá.

Etymology

The specific name *antomia* alludes to the maligned spirit or devil created by Caragabi in the mythology

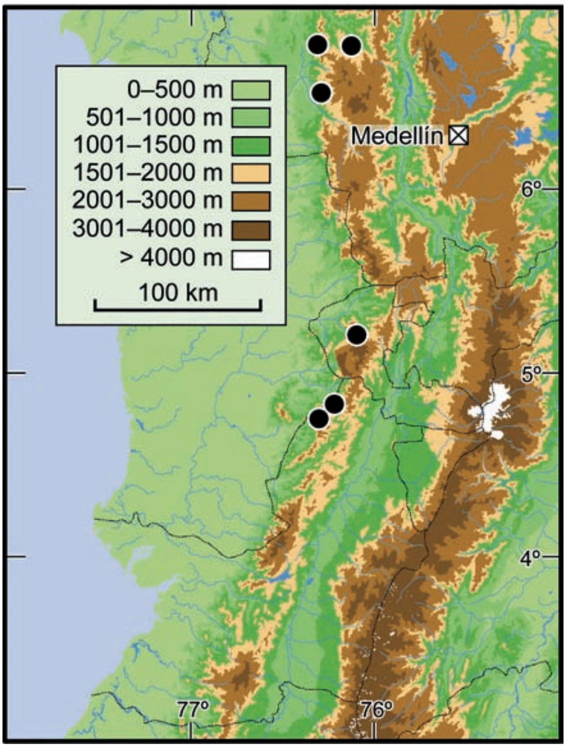

Fig. 10.22 Andean region of western Colombia, showing the localities of known occurrences of *Gastrotheca antomia*.

of the Emberá people in Chocoan Colombia (Ruíz-Carranza et al., 1997).

Remarks

I have seen only three individuals of this species, which was discovered and described by Colombian biologists after I had terminated my field work in that country.

Gastrotheca (*Amphignathodon*) *bufona* Cochran and Goin

Gastrotheca bufona Cochran and Goin, 1970:164.—Holotype: MLS 344 from Ventanas, ca. 50 km [by road] NW Yarumal, Departamento de Antioquia, Colombia.
Gastrotheca (*Amphignathodon*) *bufona*—Dubois, 1987:31.

Diagnosis

This moderately large species attains a snout–vent length of 66.8 mm. The tibia length is more than 58% of the snout–vent length, and is much longer than the foot. The interorbital distance is noticeably greater than the width of the upper eyelid. The skin on the dorsum is finely tuberculate, and lacks transverse ridges; the skin on the skull is co-ossified with the underlying cranial elements. The supraciliary processes are long and scalloped. The heel bears an elongate tubercle or long curved calcar. The tympanic annulus, if present, is granular. The first finger is equal in length to or slightly shorter than the second finger. The discs are much wider than the digits proximal to the discs. The fingers are webbed basally; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is tan, with or without dark brown spots or narrow brown transverse bars. Markings on the head consist of a narrow brown curved interocular bar; dark brown spots are present or not on the upper lip. A pale dorsolateral stripe and adjacent dark brown stripe are present or not. The flanks are tan, with or without diagonal brown marks; the venter is brown or mottled cream and brown.

Gastrotheca bufona is distinguished from other long-legged species having calcars and supraciliary processes by various combinations of characters. The calcars and supraciliary processes are much smaller in *G. andaquiensis*, *longipes*, and *walkeri*; supraciliary processes are absent in *G. angustifrons*, *weinlandii*, and *williamsoni*. The dorsal skin is smooth in *G. longipes* and areolate in *G. andaquiensis*, *walkeri*, and *williamsoni*. Transverse dermal folds are present on the dorsum in *G. angustifrons*, *cornuta*, and *dendronastes*; *G. guentheri* differs by having true teeth on the lower jaw and a snout sloping anteroventrally in profile, as opposed to the odontoids on the lower jaw and a truncate snout in *G. bufona*.

Description

The following description is based on two specimens. The body is robust; males attain a snout–vent length of 66.8 mm, and females are unknown. The head is noticeably wider than long, and nearly as wide as the body. The snout is bluntly rounded in dorsal view, slightly inclined anteroventrally, and nearly truncate in profile. The canthus rostralis is slightly curved, angular, and elevated in cross-section. The loreal region is barely concave; the lips are slightly flared. The top of the head is depressed. The interorbital distance is about 150% of the width of the upper eyelid. The internarial area is depressed. The nostrils are not protuberant, and are directed anterolaterally at a point below the anterior terminus of the canthus rostralis. The diameter of the eye is slightly greater than its distance from the nostril, and is much greater than its distance from the margin of the jaw. The tympanum is vertically ovoid, barely evident or absent, and separated from the eye by a distance about two-thirds the length of the tympanum. The tympanic annulus, if present, is tubercular, and is distinct only anteroventrally. The supratympanic fold is straight, and is co-ossified with the underlying squamosal.

The upper arm is slender; the forearm is moderately robust. A row of low ulnar tubercles is present on the ventrolateral edge of the forearm. The hand is large. The fingers are long; at least the outer fingers are webbed basally. The discs are moderately large, round, and much wider than the width of the digit proximal to the disc; the width of the disc on the third finger is 1.5 times the length of the tympanum. The relative lengths of the fingers are I ≤ II < IV < III. The subarticular tubercles are small, round, or subconical; the supernumerary tubercles are small, round, or subconical, and are numerous on the proximal segments of the third and fourth fingers. The palmar tubercle is low and trifid; the prepollical tubercle is elongately ovoid, and is devoid of nuptial excrescences. The hind limbs are long and slender. The tibia length is 58.9%–62.5% of the snout–vent length; the foot length is 48.5%–49.7% of the snout–vent length. The heel bears an elongate tubercle or a long curved pointed calcar. A few low tubercles are present on the outer edge of the tarsus; the inner tarsal fold is weak, but extends the entire length of the tarsus. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is small and elliptical. The toes are moderately long and slender. The relative lengths of the toes are I < II < III ≤ V < IV. The toes are about one-third webbed; the webbing formula is **I**2—2**II**2—3–3^{+}**III**2^{-}2—3^{+}**IV**3^{+}—2**V**. The subarticular tubercles are small and conical; the supernumerary tubercles are small, round, and present only on the proximal segments.

The skin on the dorsal surfaces of the body and limbs is finely tubercular; the skin on the head is co-ossified with the underlying dermal elements; the skin on the flanks is areolate; the skin on the throat, belly, and proximal surfaces of the thighs is granular; other surfaces are smooth. The supraciliary process on the outer margin of the upper eyelid is elongately triangular and serrate. A dermal dorsolateral fold with small triangular tubercles is evident on the anterior two-thirds of the body. Cloacal folds and tubercles are absent. The dentigerous processes of the vomers are transverse to oblique, and are narrowly separated medially at the level of the neopalatines, behind the level of the large round choanae. Each process bears four or five teeth.

COLOR IN PRESERVATIVE

Considerable variation exists in the color patterns, even in preservative.

MLS 344 from Ventanas, Departamento de Antioquia, Colombia.—The dorsum is brown, with darker brown markings consisting of transverse bars: five on each thigh and shank, three on each forearm, and four on each foot. Nine narrow transverse dark marks are present on the head and body; dark spots on the margin of the upper lip are distinct. The flanks are tan, with five dark brown diagonal marks. The throat is black; the other ventral surfaces are yellowish tan, heavily mottled with brown and black.

ICN 38086 from 6 km SW Florencia, Município Samaná, Departamento de Caldas, Colombia.—The dorsum is tan, with dark brown canthal and supratympanic stripes that are bordered above by a cream stripe; a dark brown dorsolateral stripe extends to the sacral region. Irregular narrow transverse stripes are present on the median part of the head and body, and become chevron-shaped posterior to the sacrum. The side of the head is brown, with a cream labial stripe and three dark brown spots dorsal to the stripe. The dorsal surfaces of the limbs are tan, with dark brown transverse bars: four on the forearm, six on the thigh, five on the shank, and four on the foot; the bars on the thighs extend onto the cream anterior and posterior surfaces of the thighs. The throat is black; the chest and belly are dark brown; the ventral surfaces of the limbs are tan.

COLOR IN LIFE

The following descriptions are based on color photographs of specimens from Florencia, Departamento de Caldas, Colombia, taken by the late Pedro M. Ruíz-C.

ICN 38082 (Fig. 10.23A).—The skin on the dorsum of the head, body, and limbs is pale green, with irregular creamy white spots. A dorsolateral stripe (bordered below by a narrow brown stripe), supraciliary process, labial stripe, calcar, the outer edge of the tarsus, and digits on the hands and feet are creamy white. The upper flanks are pale green; the lower flanks are creamy white, with diagonal dark brown streaks. The iris is dull cream peripherally and pale orange medially.

ICN 38084 (Fig. 10.23B).—The flanks and the dorsal surfaces of the head, body, and limbs are dull greenish tan, with darker brown markings: a narrow interocular bar, irregular transverse or diagonal marks on the dorsum, a dorsolateral stripe, diagonal marks on the flanks, and transverse bars on the limbs. The labial stripe and calcars are creamy white; the iris is dull reddish brown.

MEASUREMENTS

The measurements (in mm) of four adult males are as follows: snout–vent length 57.1–67.3 ($\bar{x} = 60.7$); tibia

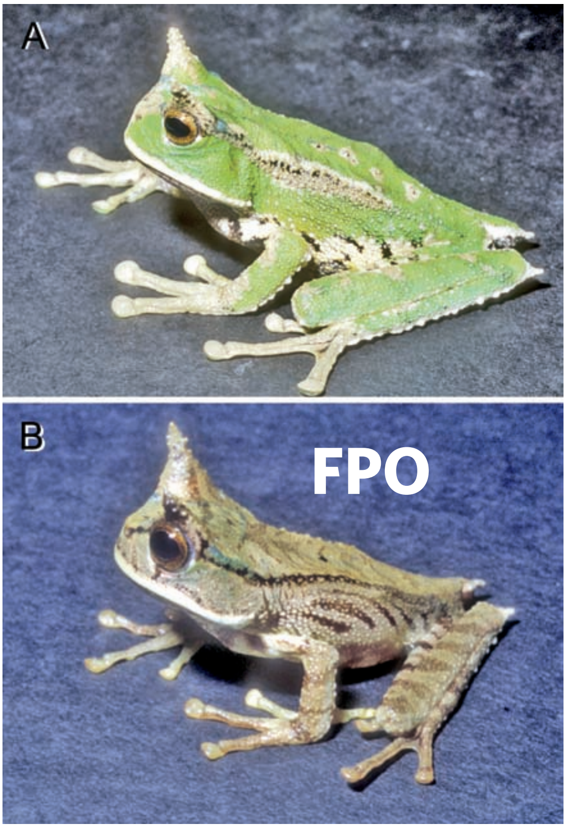

Fig. 10.23 *Gastrotheca bufona.* A: ICN 38082, male, 56.5 mm SVL, Florencia, Samaná, Caldas, Colombia. B: ICN 38084, juvenile male, 33.8 mm SVL, Florencia, Samaná, Caldas, Colombia. Photos by P. M. Ruíz-C., KUDA.

length 36.0–39.0 ($\bar{x} = 37.4$); foot length 29.3–32.1 ($\bar{x} = 30.5$); head length 20.7–22.7 ($\bar{x} = 21.6$); head width 25.0–27.8 ($\bar{x} = 26.1$); interorbital distance 8.2–10.0 ($\bar{x} = 8.9$); eyelid width 4.7–6.5 ($\bar{x} = 5.4$); internarial distance 3.2–6.1 ($\bar{x} = 4.4$); eye diameter 6.4–7.8 ($\bar{x} = 6.8$); eye–nostril distance 3.9–6.3 ($\bar{x} = 5.1$); orbit–jaw distance 4.0–5.0 ($\bar{x} = 4.4$); nostril–jaw distance 4.7–5.9 ($\bar{x} = 5.2$); tympanum diameter 3.7–4.9 ($\bar{x} = 4.2$); thumb length 12.4–15.2 ($\bar{x} = 13.1$); third finger length 21.3–23.5 ($\bar{x} = 22.5$); and width of disc on third finger 3.6–3.8 ($\bar{x} = 3.7$).

CRANIAL OSTEOLOGY

The dermal sculpturing is heterogeneous; the sphenethmoid bears a vermiform or ramus pattern, whereas the rest of the skull table has a fine pit-and-ridge pattern. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange, but lacks a distinct otic flange. A temporal arcade is absent. The frontoparietal covers the anterior epiotic eminence and the anterior part of the posterior epiotic eminence, and is partially fused to them; hence the carotid canal is partially closed, and exits the skull posteriorly adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae have long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for about half the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The postorbital process of the maxilla is massive, and has a broad horizontal articulation with the massive zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the otic plate completely articulates with and broadly overlaps the ossified crista parotica. The dorsal part of the stapedial footplate is more than three times the length of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has a blunt terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and synostotically united with the prootic. The neopalatines are widely separated medially; each bears a flange-like ventral ridge, with serrations. The pterygoid articulates with the medial side of the postorbital process of the maxilla via a long blunt dorsal ramus on the anterior ramus of the pterygoid. The vomers bear minute dentigerous processes located at the posterior margins of the choanae.

Life History

Presumably the eggs hatch into froglets.

Advertisement Call

The call is unknown.

Distribution and Ecology

This species is known only from the type locality, at an elevation of 1990 m on the northwestern slopes of the northern part of the Cordillera Central, and from an elevation of 1850 m on the eastern slopes of the Cordillera Occidental in northern Colombia (Fig. 10.24).

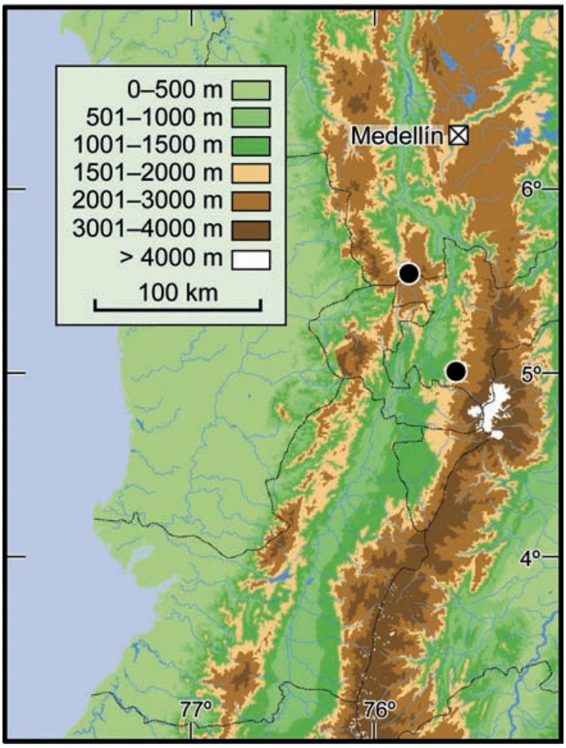

Fig. 10.24 Andean region of western Colombia, showing the localities of known occurrences of *Gastrotheca bufona*.

Conservation Status

Gastrotheca bufona is categorized as Endangered in the IUCN Red List. The species has a limited range and inhabits humid montane forests that are subject to clearing; it is not known to occur in any protected areas.

Etymology

According to Cochran and Goin (1970:167), the specific name is from the Spanish *bufón*, meaning "jester" or "clown"; the name was used in reference to the gaudy appearance of the frog.

Remarks

Duellman (1974) placed *Gastrotheca bufona* in the synonymy of *G. weinlandii*, on the basis of the description by Cochran and Goin (1970). Subsequent examination of the holotype of *G. bufona* led Duellman (1983) to recognize *G. bufona* as a distinct species. This position was substantiated by subsequent study of newly acquired specimens in ICN.

Gastrotheca (*Amphignathodon*) *cornuta* (Boulenger)

Nototrema cornutum Boulenger, 1898:124.—Holotype: BMNH 1947.2.22.49 from Cachabe, Provincia de Esmeraldas, Ecuador.

Hyla ceratophrys Stejneger, 1911:286.—Holotype: USNM 47705 from Alto Río Pequeni, Provincia de Panama, Panama. Synonymy fide Duellman, 1983:872.

Gastrotheca cornutum—Peters, 1955:339.

Gastrotheca ceratophrys—Duellman, 1966:265.

Gastrotheca cornuta—Duellman, 1983:872.

Gastrotheca (*Amphignathodon*) *cornuta*—Dubois, 1987:31.

Diagnosis

Females of this large species attain a maximum snout–vent length of 77.7 mm, and have a tibia length greater than 60% of the snout–vent length, which is much longer than the foot. The interorbital distance is slightly greater than the width of the upper eyelid. The skin on the dorsum is smooth, with transverse ridges on body; the skin on the head is not adherent to or co-ossified with the underlying cranial elements. Prominent supraciliary processes are present. The heel bears a triangular calcar. The tympanic annulus is granular. The first and second fingers are equal in length. The discs are much wider than the digits proximal to the discs. The fingers are webbed basally; on the foot the webbing extends maximally to the distal subarticular tubercles on the fourth and fifth toes. The dorsum is brown, with darker brown to black transverse bars. A pale suborbital bar and dark interocular bar are present; a pale dorsolateral stripe is absent. The flanks are uniformly dark brown; the venter is creamy brown.

This is one of three species of long-legged arboreal *Gastrotheca* having transverse dermal ridges on the dorsum. These ridges are smooth in *G. angustifrons* and smooth or weakly tuberculate in *G. cornuta*, whereas they are strongly tubercular in *G. dendronastes*, which also differs from *G. cornuta* by having granular skin on the dorsum, a distinct tubercle on the heel (instead of a small triangular calcar), and longitudinal stripes (instead of dark spots) on the flanks. *G. angustifrons* differs from *G. cornuta* by lacking calcars and supraciliary processes. Other species that have large supraciliary processes (*G. bufona*, *guentheri*, and *weinlandii*) lack transverse dermal ridges on the dorsum, and have much larger calcars and co-ossified skulls.

Description

The following description is based on 26 adults. The body is moderately robust; the largest male has a snout–vent length of 81.1 mm, and 76.9 mm in the largest female. The head is distinctly casqued in larger individuals, not co-ossified, slightly wider than long, and nearly as wide as the body. The snout is bluntly rounded in dorsal view, abruptly inclined anteroventrally, and nearly truncate in profile; it barely extends beyond the anterior margin of the jaw. The canthus rostralis is angular in cross-section, and is slightly curved. The loreal region is distinctly concave; the lips are rounded. The top of the head is slightly depressed, owing to the upward flaring of the lateral margins of the frontoparietals. The interorbital distance is about 135% of the width of the upper eyelid. The internarial area is flat. The nostrils are slightly protuberant, and are directed laterally at a point below the anterior terminus of the canthus rostralis and above the anterior margin of the lower lip. The diameter of the eye is slightly greater than its distance from the nostril, and is about 60% greater than its distance from the margin of the jaw. The tympanum is vertically ovoid, and is separated from the eye by a distance twice the length of the tympanum. The tympanic annulus is indistinct and tubercular. The supratympanic fold is weak, extends directly posteriorly from the posterior corner of the orbit, and obscures the upper edge of the tympanum.

The arm is moderately slender; ulnar tubercles are absent. The hand is large. The fingers are long and slender; the outer fingers are webbed basally. The discs on the fingers are large, slightly broader than long, and much wider than the width of the digit; the diameter of the disc on the third finger is nearly twice the length of the tympanum. The relative lengths of the fingers are I = II < IV < III. The subarticular tubercles are large and round; the supernumerary tubercles are small, subconical, and numerous on the proximal segments. The palmar tubercle is low and bifid; the prepollical tubercle is elliptical; nuptial excrescences are absent. The hind limb is long and slender. The tibia length is about 64% of the snout–vent length; the foot length is about 47% of the snout–vent length. A small triangular calcar is present on the heel in 80% of the specimens. Tarsal tubercles and a tarsal fold are absent. The inner metatarsal tubercle is small, elliptical, and barely visible from above; an outer metatarsal tubercle is absent. The toes are long and slender. The relative lengths of the toes are I < II < III < V < IV. The toes are about two-thirds webbed; the webbing formula is **I**(1–2^{-})—2**II**1—2**III**2—(1–2)**IV**(1–2)—(1–1½)**V**. The subarticular tubercles are moderately large and round; the supernumerary tubercles are small, subconical, and indistinctly present only on the proximal segments.

The skin on the dorsal surfaces of the head, body, and limbs is smooth; the skin on the flanks is areolate; the skin on the throat, belly, and posteroventral surfaces of thighs is granular; other surfaces are smooth. There are 8–12 low smooth or weakly tuberculate transverse ridges on the head and body. The anteriormost ridge usually is between the orbits and extends onto the eyelids, but a weak ridge exists anterior to the eyes in three specimens; the ridges are discontinuous in five specimens. A prominent triangular supraciliary process is present on the margin of the upper eyelid. A pair of large tubercles is present ventrolateral to the cloaca. The pouch opening is V-shaped, with the anterior border at the level of the sacrum. The dentigerous processes of the vomers are greatly elevated, slightly inclined posteromedially, and narrowly separated medially at a level between the moderately large round choanae. Each process bears seven to nine teeth.

COLOR IN PRESERVATIVE

The dorsum is tan, dull gray, or dark brown, with 8–15 darker brown or black narrow transverse lines, usually associated with the transverse dermal ridges. A dark canthal stripe is absent. In most specimens a narrow dark brown dorsolateral line begins above the tympanum and extends to midlength of the body. Dark flecks are present on the dorsum in 10 specimens (33%). The flanks are colored like the dorsum, with diffuse dark spots in 57%. The dorsal surfaces of the limbs are colored like the body, with dark brown transverse bars: five or six on each thigh, four or five on each shank, and three or four on each foot. The anterior surfaces of the thighs are pale, with dark vertical bars in 90%; the posterior surfaces of the thighs are brown, with darker brown vertical bars in 33%. A distinct creamy white suborbital bar is present in 50% (two bars in 7%). A dark brown patch in the cloacal region is bordered above by a narrow transverse creamy white stripe; one (43%) or two (57%) pairs of pale spots are present ventrolateral to the cloacal opening. The venter is dull creamy brown, with grayish-brown flecks in 23% of the specimens; the outer toes and webbing are dark brown (77%) or tan (23%).

COLOR IN LIFE

The dorsum is tan or brown, with darker brown transverse markings on the head, body, and limbs. When active at night, the frogs usually are pale yellowish tan, grayish tan, or olive tan, with creamy white flanks and belly. By day the dorsum is darker brown; the flanks are creamy tan, with brown markings; the throat is brown, and the belly and ventral surfaces of the limbs are pinkish tan or pale brown. A cream subocular spot

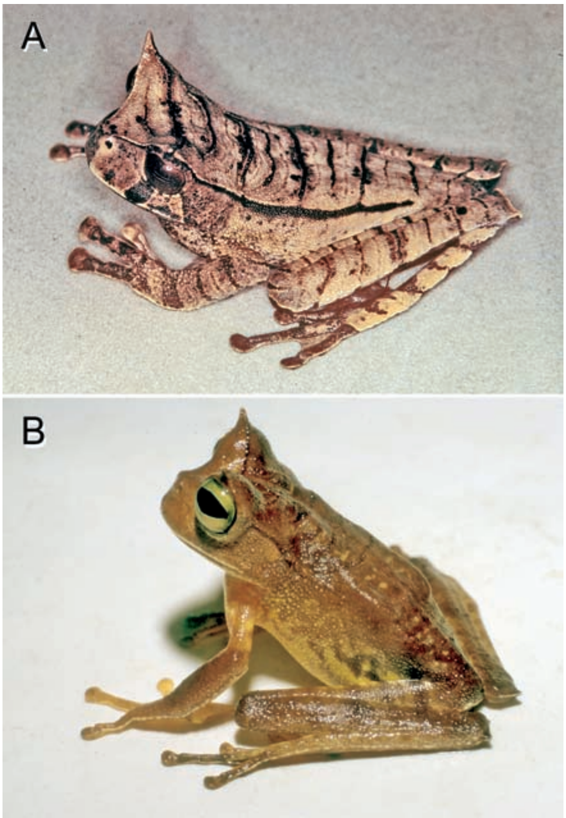

Fig. 10.25 *Gastrotheca cornuta.* A: KU 101535, male, 76.1 mm SVL, Río Claro, 910 m, Bocas del Toro, Panama. B: AMNH 88204, juvenile, Quebrada Guanguí, Cauca, Colombia. Photos by W. E. Duellman (A) and C. W. Myers (B), KUDA.

usually is evident only by day. The supracloacal stripe is cream. Variation in life is documented by the following descriptions.

KU 101535 from Río Changena, Provincia de Bocas del Toro, Panama.—When found at night, the frog had a pale yellowish-tan dorsum, with brown transverse ridges and bars on the hind limbs and the cloacal region; the flanks and belly were creamy white. By day the frog became brown above, with darker brown markings (Fig. 10.25A); the flanks changed to creamy tan, with brown venation; the throat was brown. The belly and undersides of the limbs were pinkish tan. The bars on the lips were brown, with a creamy yellow subocular spot. Later the frog changed to olive tan dorsally; the supracloacal stripe became yellow. The webbing was brown throughout. The iris was bronze peripherally and olive green medially; the pupil was horizontally elliptical; the palpebrum was clear. The tongue was creamy yellow (W. E. Duellman field notes, 20 May 1966).

AMNH 90981–84 from Cerro Tacarcuna, Provincia de Darién, Panama.—The dorsum varied from yellowish brown to brown or dark green; the flanks and anterior and posterior surfaces of the thighs had yellow or pale yellow mottling, of variable distinctness. The subocular spots were white; the ventral surfaces were brown. The iris was brown medially, becoming pale brown peripherally (C. W. Myers field notes, 24–27 January 1975.

AMNH 88204 from Quebrada Ganquí, Departamento de Cauca, Colombia.—The posterior surfaces of the thighs were banded dark brown and golden yellow (Fig. 10.25B). The venter was pale yellowish-orange; the iris was pale olive green (C. W. Myers field notes, 10–12 February 1973).

MEASUREMENTS

No significant differences in measurements exist between the sexes, except in disc width (Table 10.7).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous fine pit-and-ridge pattern. The nasals articulate medially, and are fused to one another and to the sphenethmoid posteriorly; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a narrow supraorbital flange, but lacks a distinct otic flange. A temporal arcade is absent. The frontoparietal covers but is not fused to the anterior epiotic eminence; therefore the carotid canal is open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae bear long spinous medial processes. A notch distinguishes the preorbital process from the facial process of the maxilla, which has a short articulation with the nasal; the pars facialis is distinctly separated from the alary process of the premaxilla, but has only a slight overlap with the dental process of the premaxilla. The quadratojugal is long. The postorbital process of the maxilla is not visible; there is a firm articulation between the distomedial branch of the slender zygomatic process of the squamosal and the anterior ramus of the pterygoid. The head of the squamosal bears a narrow crest; the otic plate completely articulates with and moderately overlaps the ossified crista parotica. The relative sizes of the dorsal and ventral parts of the stapedial footplate, when viewed in posterior aspect, could not be determined. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestram, and has a

Table 10.7 Univariate statistics for adults of *Gastrotheca cornuta*

	Males ($n = 30$)			Females ($n = 8$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	66.7	44.1–81.1	9.35	70.8	51.2–77.4	9.36
Tibia length	41.8	28.9–49.6	5.36	45.0	30.5–49.1	6.37
Foot length	30.7	21.0–38.7	5.17	33.5	22.6–37.5	5.05
Head length	23.0	16.6–26.8	3.21	24.2	17.2–26.1	3.09
Head width	25.5	18.1–30.3	3.27	27.2	19.8–30.6	3.61
Interorbital distance	8.1	4.4–10.4	1.76	8.1	5.2–9.9	1.64
Eyelid width	6.1	4.1–7.6	0.97	6.4	4.4–7.4	1.05
Internarial distance	4.5	2.7–6.3	0.96	4.3	3.0–5.8	0.71
Eye diameter	7.1	4.7–8.8	1.19	7.4	5.8–8.1	0.77
Eye–nostril distance	6.2	4.5–7.6	1.08	6.3	4.0–8.1	1.24
Orbit–jaw distance	3.9	2.5–4.6	0.58	3.9	2.7–5.6	1.12
Nostril–jaw distance	4.8	3.2–6.2	0.89	5.2	3.5–5.8	0.91
Tympanum diameter	3.5	1.5–4.5	0.84	3.0	1.6–4.0	0.88
Thumb length	14.0	8.2–16.6	2.40	15.2	8.6–18.2	3.15
Third finger length	22.8	15.6–28.0	3.75	24.7	16.4–27.5	3.68
Disc width	3.7	2.6–4.5	0.63	4.2	2.7–5.2	0.81

blunt terminus posterior to the level of the neopalatines. The sphenethmoid is ossified posterior to the midlength of the orbit, but is not synostosed with the prootic. The neopalatines are widely separated medially, and bear a low irregular ventral ridge; they do not form the posterior margins of the choanae. The pterygoid articulates with the squamosal via a ventromedial process of the zygomatic ramus of the latter; the pterygoid lacks a distinct dorsal ramus on its anterior ramus, and instead has a broad low dorsal expansion. The vomers bear moderately large dentigerous processes located between the anterior quadrants of the choanae.

Life History

This species has been the subject of captive breeding at the Atlanta Botanical Garden in Georgia and at El Valle Amphibian Conservation Center in Panama (Gagliardo et al., 2010). One completely documented breeding event required three hours from the time amplexus was initiated until the last egg was placed in the pouch. Shortly after amplexus occurred, the male inflated and deflated his lungs several times, and angled his hind legs upward so that his feet were between the female's cloaca and the opening of the brood pouch. Using his toes, the male rubbed a gel-like substance (presumably from the male's cloaca) over the lower back and pouch of the female. He continued this activity while maintaining cycles of lung inflation and deflation for about 45 minutes. The female arched her back, so her cloaca was directed upward, nearly in contact with the male's cloaca. More than two hours after amplexus was initiated, the first egg appeared, and five eggs emerged during the following 31 minutes. The male used his feet to position the eggs and push them into the brood pouch.

The eggs undergo direct development in the brood pouch. Brooding females have been found in January and July in Panama, and in May and August in Colombia. The ova are 9.2–17.0 mm in diameter. A female from Laguna, Provincia de Darién, Panama, contained 10 eggs in Stage 34; the ova were 9.2 mm in diameter. A female from Tacarcuna, Provincia de Darién, Panama, prematurely expelled embryos in Stage 45; these had diameters of about 13.3 mm. A female from El Tambo, Departamento de Cauca, Colombia, contained five eggs in Stage 42 that were about 17.0 mm in diameter. A female with a snout–vent length of 72.5 mm from Cerro Torrá, Departamento de Chocó, Colombia, contained 10 hatchling embryos having snout–vent lengths of 16.5 mm. One female from Costa Rica contained seven eggs that were 9.8 mm in diameter, and another contained nine embryos (Savage, 2002). Females that bred in captivity produced 23 and 14 young after gestation periods of 60–80 days.

Advertisement Call

Although this species lacks vocal slits (Tyler and Duellman, 1995), it does vocalize. The call is a loud "bop." Although usually only one note is produced, sometimes a frog produces two or three notes in quick succession. Intervals between calls usually are several minutes. In one call (KU Tape No. 595)—recorded at Río Claro, near its junction with Río Changena, Provincia de Bocas del Toro, Panama, at 2100 hours on 23 May 1966, at an air temperature of 18.3°C—the duration of each note is 0.08 second, and the interval between notes is 0.60 second. Each note noticeably diminishes in pitch and consists of three harmonics at about 800, 1600, and 2400 Hz, of which the lowest harmonic is the dominant frequency. Another recording (KU Tape No. 732) was made at the Estación Biológica Río Palenque, 220 m, 56 km north of Quevedo, Provincia de Los Ríos, Ecuador, at 2030 hours on 31 March 1975, at a temperature of 23.5°C.

Distribution and Ecology

Gastrotheca cornuta has a wide distribution, encompassing the Caribbean slopes (90–1000 m) of eastern Costa Rica and Panama and the Pacific slopes (100–1000 m) of southern Colombia and northwestern Ecuador (Fig. 10.26). A hiatus of about 500 km in central and northern Chocoan Colombia exists between the known occurrence of this species in Central America and in western South America. This gap may be an artifact of sampling, inasmuch as relatively little collecting has been done in that part of Colombia; *G. angustifrons* has been taken in the region where *G. cornuta* has not been found. The species inhabits lowland tropical rainforest

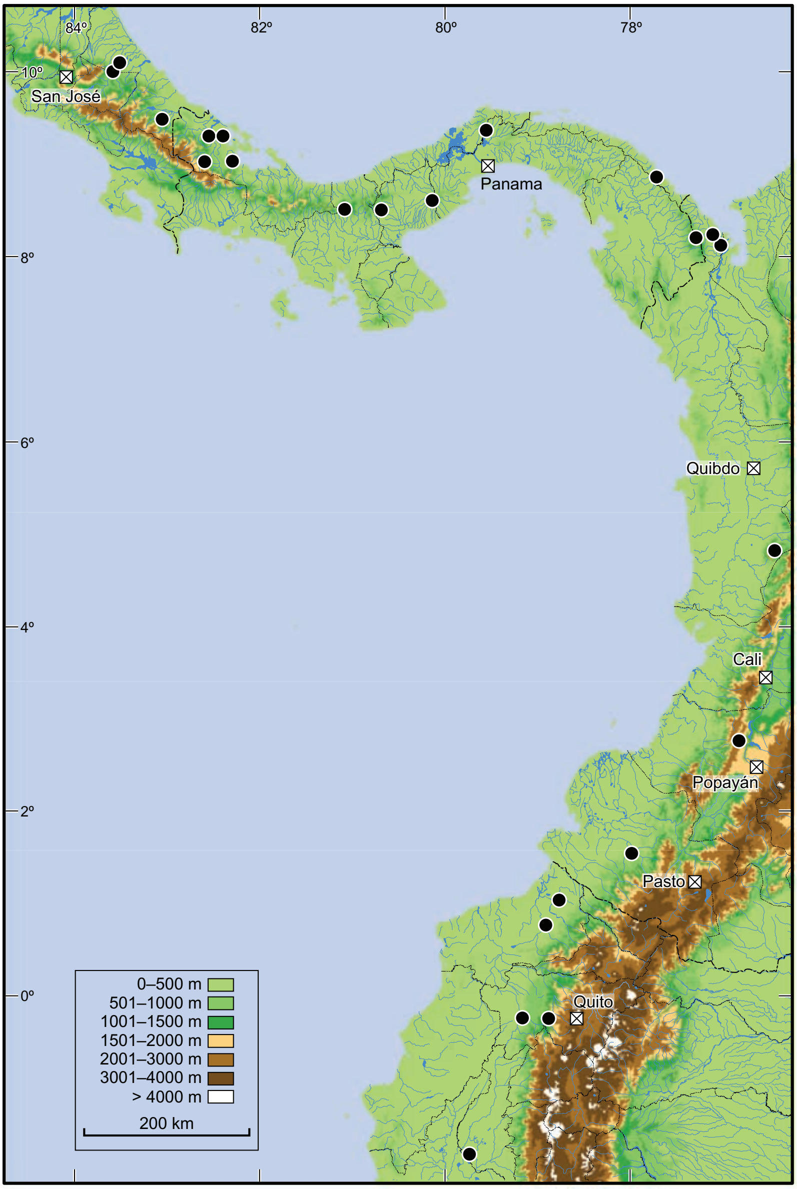

Fig. 10.26 Northwestern South America and adjacent Central America, showing the localities of known occurrences of *Gastrotheca cornuta.*

and low montane rainforest, where it seems to live primarily in the canopy. Although many individuals can be heard calling from the upper branches (estimated to be 20–35 m above the ground) of trees, few individuals are observed on lower branches.

Conservation Status

This species is listed as Endangered in the IUCN Red List. It has disappeared from Costa Rica and western Panama, where these declines have been associated with the disease chytridiomycosis (Lips et al., 2006). According to the Red List, this disease is also present in the lowlands of western Ecuador, and it may have contributed to the substantial declines of this species in Ecuador, which is currently associated with extensive habitat loss. Areas of forest close to the type locality of "Cachabé" [= Cachabí], Provincia de Esmeralda, Ecuador, have now been deforested, and no *Gastrotheca cornuta* are present there. Possibly the species also has declined in Colombia, with few records and ongoing serious habitat fragmentation in Departamentos de Cauca and Nariño. In addition to disease, other major threats are deforestation for agricultural development, illegal crops, logging, human settlement, and pollution resulting from the spraying of illegal crops.

Etymology

The specific name is the Latin adjective *cornutus*, meaning "horned." The name refers to the prominent supraciliary processes, which have been termed eyelid horns.

Remarks

The largest individuals are from Costa Rica: eight males have snout–vent lengths of 67.0–81.1 mm ($\bar{x}$ = 73.6), and a single female has a snout–vent length of 73.6 mm (Duellman 2001). Also, Costa Rican specimens have the most transverse dermal ridges, 11–14 ($\bar{x}$ = 11.4). The similarities between *Gastrotheca cornuta* and *G. angustifrons* have been discussed in the account of the latter species; a stepwise discriminant analysis of morphometric data correctly classified 90% of the specimens (Fig. 10.16).

As is evident from the preceding descriptions of coloration in life, noticeable differences exist among the specimens assigned to *Gastrotheca cornuta*. The differences in iris color are perplexing, because geographic variation in this character is most unusual. A cluster analysis was performed, in order to ascertain if a geographic pattern exists in the variation in structural characters (Fig. 10.27). Although five individuals from the Pacific slopes of southern Colombia and north-

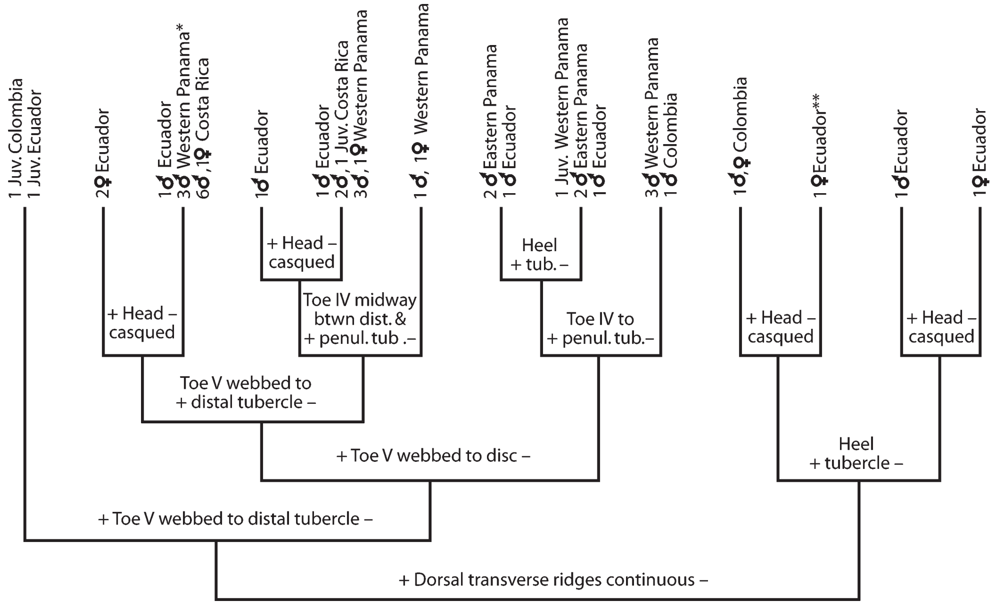
1 Juv. Colombia
1 Juv. Ecuador
2♀ Ecuador
1♂ Ecuador
3♂ Western Panama*
6♂, 1♀ Costa Rica
1♂ Ecuador
1♂ Ecuador
2♂, 1 Juv. Costa Rica
3♂, 1♀ Western Panama
1♂, 1♀ Western Panama
2♂ Eastern Panama
1♂ Ecuador
1 Juv. Western Panama
2♂ Eastern Panama
1♂ Ecuador
3♂ Western Panama
1♂ Colombia
1♂, ♀ Colombia
1♀ Ecuador**
1♂ Ecuador
1♀ Ecuador
+ Head – casqued
Heel + tub. –
+ Head – casqued
Toe IV midway btwn dist. & + penul. tub .–
Toe IV to + penul. tub.–
+ Head – casqued
+ Head – casqued
Toe V webbed to + distal tubercle –
+ Toe V webbed to disc –
Heel + tubercle –
+ Toe V webbed to distal tubercle –
+ Dorsal transverse ridges continuous –

Fig. 10.27 Phenogram of a cluster analysis, showing the geographic distribution of the character states of external morphological characters in 41 specimens of *Gastrotheca cornuta*. The plus sign indicates the presence of the character, and the minus sign notes that the statement does not apply in descendant individuals. Eastern Panama includes only the provinces of Darién and San Blas; western Panama includes the rest of the country. The single asterisk denotes the holotype of *Hyla ceratophrys*; the double asterisk denotes the holotype of *Nototrema cornutum*.

western Ecuador are distinguished by discontinuous transverse dermal ridges, four other specimens from that region are grouped with specimens from Central America, all of which have continuous transverse dermal ridges. Until new definitive evidence is available to distinguish more than one species, the placement of *Hyla ceratophrys* Stejneger, 1911, in the synonymy of *Nototrema cornutum* Boulenger, 1898, is followed, as suggested by Duellman (1983).

Gastrotheca (*Amphignathodon*) *dendronastes* Duellman

Gastrotheca dendronastes Duellman, 1983:868.—Holotype: KU 169381 from Río Calima, 1.5 km [by road] W Lago Calima, 1230 m, Departamento de Valle del Cauca, Colombia.

Gastrotheca (*Amphignathodon*) *dendronastes*—Dubois, 1987:31.

Diagnosis

In this moderately large species, adults attain a snout–vent length of 79.5 mm; the tibia length is more than 60% of the snout–vent length, and is much longer than the foot. The interorbital distance is slightly greater than the width of the upper eyelid. The skin on the dorsum is finely granular, with scattered tubercles, and is not adherent to or co-ossified with the skull; tuberculate transverse dorsal ridges are present. A supraciliary process is present; the heel bears a conical tubercle. The tympanic annulus is granular. The first finger is longer than the second. The discs are much wider than the digits. The fingers are unwebbed; on the foot the webbing extends maximally to a point midway between the antepenultimate and penultimate subarticular tubercles on the fourth toe and the distal subarticular tubercle on the fifth toe. The dorsum is tan, with irregular brown spots. Markings on the head consist of a pale suborbital bar, and a dark canthal stripe and interocular bar. There is no pale dorsolateral stripe. The flanks are brown, with longitudinal cream stripes; the venter is cream, with brown spots.

Of the three species having transverse dermal ridges on the dorsum, *Gastrotheca dendronastes* is unique in having strongly tubercular, instead of smooth, ridges, as in *G. angustifrons* and *G. cornuta*. Furthermore, the skin on the dorsum is granular in *G. dendronastes* and smooth in the other two species. *G. angustifrons* differs from *G. dendronastes* by lacking a supraciliary process and tubercle on the heel. The presence of longitudinal dark stripes on the flanks distinguishes *G. dendronastes* from all other long-legged arboreal *Gastrotheca*, except some specimens of *G. guentheri*, in which the skin on the head is co-ossified with the underlying dermal elements. Also, *G. guentheri* has large calcars, true teeth on the dentary, and lacks transverse dermal ridges on the dorsum.

Description

The following description is based on 22 specimens. The body is robust; males attain a snout–vent length of 79.5 mm, and 73.5 mm in females. The head is not casqued, nor is the skin co-ossified with the underlying cranial elements. The head is wider than long, and slightly wider than the body. The snout is rounded in dorsal view, and is abruptly inclined anteroventrally from the nostrils to the lip in profile; it barely protrudes beyond the margin of the jaw. The canthus rostralis is slightly angular in cross-section, and is curved. The loreal region is concave; the lips are moderately flared. The top of the head is slightly depressed. The interorbital distance is about 110% of the width of the upper eyelid. The internarial area is slightly convex. The nostrils are barely protuberant, directed anterolaterally at a point below the anterior terminus of the canthus rostralis and barely posterior to the anterior margin of the lower jaw. The diameter of the eye is only slightly greater than its distance from the nostril, and is about 20% greater than its distance from the margin of the jaw. The tympanum is vertically ovoid, separated from the eye by a distance about twice the length of the tympanum. The tympanic annulus is distinct and tubercular. The supratympanic fold is moderately heavy, obscures the upper edge of the tympanum, and extends from the posterior corner of the orbit to a point just posterior to the tympanum, where it bifurcates into one ridge extending posteriorly as a dorsolateral fold onto the anterior part of the body, and another curving ventral to a point above the insertion of the arm.

The arm is moderately robust; a row of low ulnar tubercles is present on the ventrolateral surface of forearm. The hand is large. The fingers are long, slender, and unwebbed. The discs are moderately large and round; the width of the disc on the third finger is noticeably greater than the length of the tympanum. The relative lengths of the fingers are I > II = IV < III. The subarticular tubercles are moderately large, low, and round; the supernumerary tubercles are indistinct, and are present only proximally. The palmar tubercle is low and indistinct; the prepollical tubercle is elongate and ovoid; nuptial excrescences are absent. The hind limb is long and slender. The tibia length is about 64% of the snout–vent length; the foot length is about 52%

of the snout–vent length. A conical tubercle is present on the heel. Tarsal tubercles and folds are absent. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is moderately small, low, elliptical, and not visible from above. The toes are long and slender. The relative lengths of the toes are I < II < III < V < IV. The toes are about two-thirds webbed; the webbing formula is **I**2—2**II**1—1**III**(1–2)—(2½–3)**IV**(2½–3)—(1–2) **V**. The subarticular tubercles are moderately large and round; the supernumerary tubercles are small, indistinct, and present only on the proximal segments.

The skin on the dorsum of the body is finely granular, with scattered round tubercles and 9–12 transverse tubercular ridges. The first ridge is between the anterior corners of the orbits, the second is across the eyelids, the third is in the intertympanic region, and the last is at the level of the groin. The skin on the flanks is deeply areolate; the skin on the belly and posteroventral surfaces of the thighs is granular; the other ventral surfaces are smooth. A triangular supraciliary process is present on the margin of the upper eyelid. Round to conical tubercles are present in the tympanic region. A pair of tubercles lie just below the cloacal opening; a pair of larger tubercles is present ventrolateral to the cloacal opening. The pouch opening is V-shaped, with the anterior border of the pouch at the level of the sacrum. The dentigerous processes of the vomers are protuberant, transverse between the round choanae, and narrowly separated medially. Each process bears six to eight teeth.

COLOR IN PRESERVATIVE

The dorsal surfaces of the head and body are olive tan to reddish brown, with small dark brown irregular markings. These markings are coalesced into irregular transverse bars on the head (including a distinct interorbital mark) in all specimens, as well as on the body in all but three specimens; in the latter specimens the dark pigment is more extensive middorsally, thereby obscuring the transverse pattern. The side of the head is pale brown, with dark brown vertical bars on the upper lip; areas between the bars are pale brown, except below the orbit, where two areas are white, resulting in two pale suborbital bars. The dorsal surfaces of the limbs are tan, with dark brown transverse bars: two on the upper arm, two or three broad bars on the forearm (with narrow dark lines between the broad bars in six specimens), five or six each on the thighs and shanks, four or five on the tarsi, and at least two on the outer fingers and toes. The anterior surfaces of the thighs are pale brown, with dark brown vertical bars continuous with those on the dorsal surfaces. The posterior surfaces of the thighs are pale brown, with or without faint irregular dark marks; the outer toes are colored like the inner ones. The flanks are either dark brown, with two or three longitudinal cream to pale tan stripes, or cream to pale tan, usually with two longitudinal brown stripes, the lower one of which is fragmented in some individuals. A dark brown patch in the cloacal region is bordered above by a narrow transverse white line; a narrow transverse white stripe is present on the heel. White spots are present ventrolateral to the cloaca in 90% of the specimens: two spots on each side in 55%, and one spot on each side in 35%. The dark brown tip of the snout is continuous with a narrow canthal stripe. The venter is cream to tan, with small brown spots or flecks that are most conspicuous on the chest and thighs.

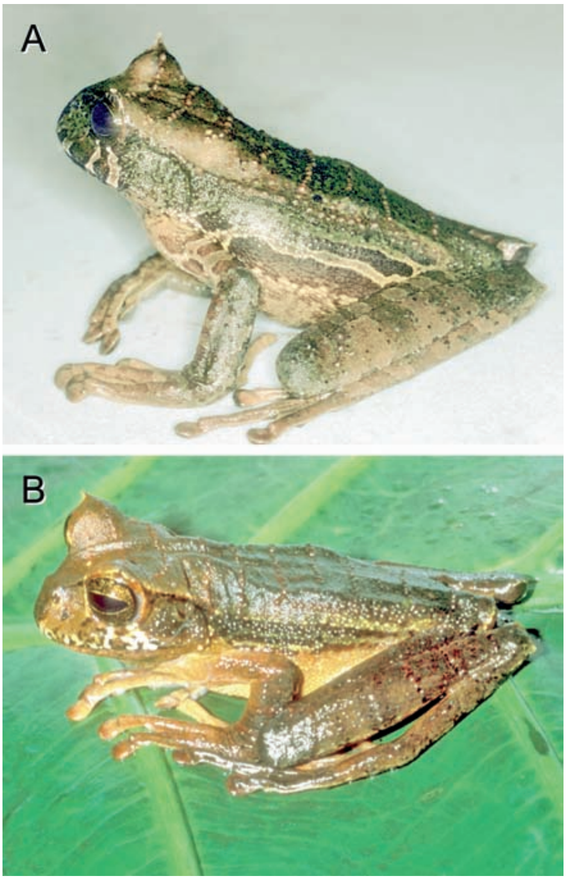

Fig. 10.28 *Gastrotheca dendronastes.* A: KU 169381 (holotype), male, 63.5 mm SVL, Río Calima, 1.5 km W Lago Calima, Valle de Cauca, Colombia. B: USNM 258936, male, 61.3 mm SVL, Río Faisanes, Pichincha, Ecuador. Photos by W. E. Duellman (A) and R. W. McDiarmid (B), KUDA.

COLOR IN LIFE

At night the dorsum is tan, with slightly darker brown transverse markings. By day the dorsum is pale brown to olive tan, with reddish-brown transverse marks and irregular green flecks (Fig. 10.28A). The flanks are olive green to dark brown, with cream longitudinal stripes bordered by dark brown. The posterior surfaces of the thighs are pale brown. The labial bars, supracloacal stripe, and heel stripes are cream. The webbing is reddish brown; the venter is creamy yellow, with reddish-brown flecks. The iris is dull bronze, with fine black reticulations (W. E. Duellman field notes on topotypes, 13–15 September 1974 and 31 May–1 June 1975). Some other specimens are more olive brown, and lack green flecks (Fig. 10.28B).

MEASUREMENTS

No sexual dimorphism in any measurement was revealed by an ANOVA. The measurements (Table 10.8) do not include the largest specimen, a male with a snout–vent length of 79.5 mm, which was skeletonized before all measurements were taken. Only three adult females are known; presumably females attain a size equal to or greater than the males.

CRANIAL OSTEOLOGY

The dermal sculpturing is heterogeneous; the sphenethmoid bears a vermiform or ramus pattern, whereas the rest of the skull table has a coarse pit-and-ridge pattern. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a narrow supraorbital flange, but lacks a distinct otic flange. A temporal arcade is absent. The frontoparietal covers but is not fused to the anterior epiotic eminence; therefore the carotid canal is open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae bear long spinous medial processes. A notch distinguishes the preorbital process from the facial process of the maxilla, which has a short articulation with the nasal; the pars facialis is distinctly separated from the alary process of the premaxilla, but has only a slight overlap with the dental process of the premaxilla. The quadratojugal is long. The postorbital process of the maxilla is massive, and has a broad diagonal articulation with the wide zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the otic plate completely articulates with and moderately overlaps the ossified crista parotica. The dorsal part of the stapedial footplate is more than three times the length of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has a blunt terminus posterior to the level of the neopalatines. The sphenethmoid is ossified posterior to the midlength

Table 10.8 Univariate statistics for adults of *Gastrotheca dendronastes*

	Males (n = 21)			Females (n = 3)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	66.9	39.8–74.8	7.92	69.3	61.9–73.5	6.45
Tibia length	42.7	25.6–47.9	5.39	45.6	42.3–47.8	2.91
Foot length	34.9	20.8–41.5	4.80	37.0	35.0–39.2	2.10
Head length	23.8	15.8–27.1	2.88	24.6	22.9–26.3	1.70
Head width	26.0	17.0–28.7	2.70	27.1	25.4–28.6	1.61
Interorbital distance	6.7	3.8–8.1	0.93	7.2	6.7–7.9	0.64
Eyelid width	6.0	4.3–7.4	0.88	6.3	5.4–7.0	0.81
Internarial distance	4.3	2.7–5.2	0.58	4.4	4.9–4.9	0.50
Eye diameter	6.6	4.4–7.8	0.91	6.4	5.8–6.8	0.53
Eye–nostril distance	6.0	4.0–6.7	0.62	6.3	6.3–6.4	0.06
Orbit–jaw distance	5.0	3.4–6.1	0.82	5.0	4.2–5.6	0.72
Nostril–jaw distance	5.7	3.4–6.9	0.77	5.6	5.8–6.3	0.40
Tympanum diameter	3.1	2.2–3.7	0.44	3.0	2.9–3.0	0.06
Thumb length	15.8	9.8–17.8	2.06	16.8	16.2–17.5	0.65
Third finger length	24.6	15.3–28.9	3.13	26.4	24.7–27.6	1.53
Disc width	4.2	1.7–4.8	0.52	4.3	4.1–4.5	0.21

of the orbit, but is not synostosed with the prootic. The neopalatines are narrowly separated medially, and bear a flange-like ventral ridge. The pterygoid articulates with the squamosal via a ventromedial process of the zygomatic ramus of the latter; the pterygoid lacks a distinct dorsal ramus on its anterior ramus, and instead has a broad low dorsal expansion. The vomers bear moderately large dentigerous processes located between the middle quadrants of the choanae.

Life History

One female contained 11 ovarian eggs that were 9 mm in diameter. The ovarian complement and size of the ova are comparable to those of *Gastrotheca cornuta* and *G. guentheri*, both of which have direct development. Thus it is safe to assume that direct development also occurs in *G. dendronastes*. The breeding season may be long, as evidenced by the presence of juveniles in March and December at Río Calima in Colombia, and in January and May at Río Faisanes in Ecuador.

Advertisement Call

The call is a loud chuckle-like sound, followed by three to four "clucks." No recording is available.

Distribution and Ecology

This species is known from cloud forest at elevations of 1230–1380 m on the Pacific slopes of the Cordillera Occidental in southern Colombia and northern Ecuador, and from 1700 m in the northern part of the Cordillera Central in Colombia (Fig. 10.29). All individuals have been found at night, in ravines containing streams. Most adults have been observed 2–5 m above the ground, on branches of trees or stems of giant *Heliconia*.

Conservation Status

According to the IUCN Red List, *Gastrotheca dendronastes* is categorized as Threatened. It is listed as rare in Ecuador but still common in Colombia, where it occurs in several protected areas.

Etymology

The specific name is derived from the Greek *dendron*, meaning "tree," and the Greek *nastes*, meaning "inhabitant." The name was used in reference to the arboreal habits of this species (Duellman, 1983).

Remarks

Although *Gastrotheca dendronastes* is distinguished from other long-legged arboreal *Gastrotheca* on the Pacific versant of South America by several characters of external structure and coloration, it is similar in size and proportions to the other species. A stepwise discriminant analysis of morphometric data distinguished *G. dendronastes* from *G. angustifrons* and *G. cornuta* only by the nostril–jaw distance (Fig. 10.15).

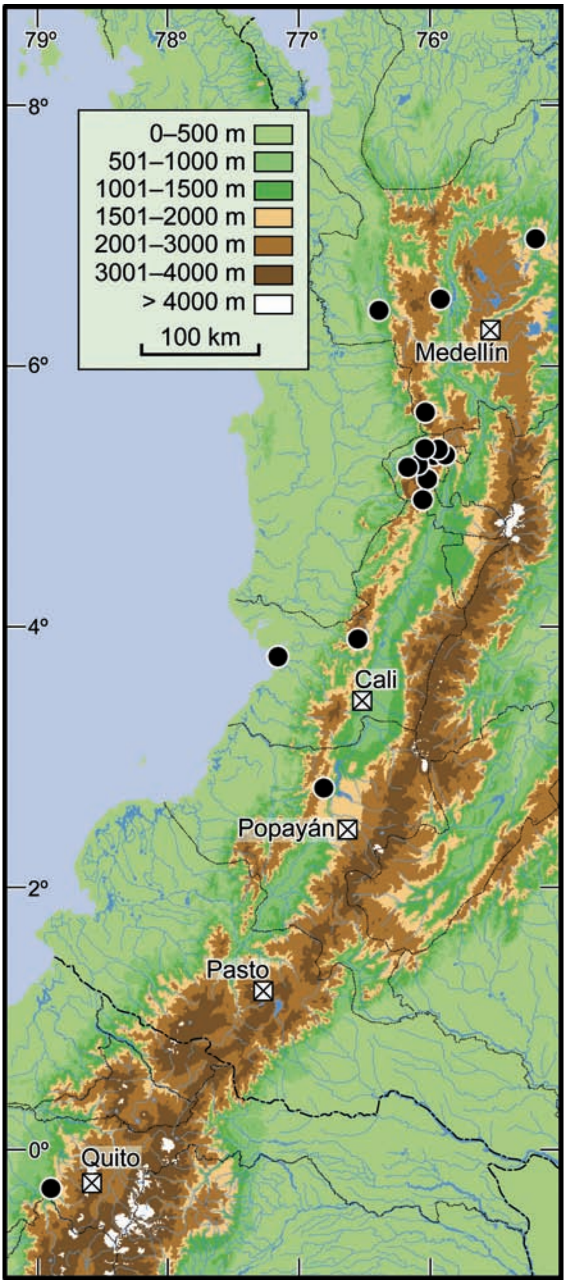

Fig. 10.29 Western Colombia and Ecuador, showing the localities of known occurrences of *Gastrotheca dendronastes.*

Gastrotheca (Amphignathodon) guentheri (Boulenger)

Amphignathodon guentheri Boulenger, 1882:450.—Holotype: BMNH 1946.9.7.28 from Intag, Provincia de Imbabura, Ecuador.

Gastrotheca guentheri—Duellman, Maxson, and Jesiolowski, 1988:531.

Diagnosis

In this large species, adults attain a snout–vent length of 82.0 mm. The tibia length is more than 60% of the snout–vent length. and is much longer than the foot. The interorbital distance is noticeably greater than the width of the upper eyelid. The skin on the dorsum is granular; the skin on the head is co-ossified with the skull; transverse dermal ridges are absent. Elongate triangular supraciliary processes are prominent. The heel bears a triangular calcar. The tympanic annulus is granular. The first and second fingers are equal in length; the discs on the fingers are much wider than the digits. The fingers are unwebbed; on the toes, the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth finger and the penultimate subarticular tubercle on the fifth toe. The dorsum is either green or brown, with darker blotches, or dark brown to black, with pale flecks. A dark canthal stripe is present; an interorbital bar may be present. A pale dorsolateral stripe also may be present. The flanks are tan, with or without a pale ventrolateral stripe; the venter is uniformly creamy brown.

Gastrotheca guentheri is distinguished from all other anurans by the presence of true teeth on the dentary. In contrast to other long-legged arboreal *Gastrotheca*, it differs from *G. angustifrons*, *cornuta*, and *dendronastes* by lacking transverse dermal ridges on the dorsum. It differs from all other species (except *G. bufona* and *G. weinlandii*) by having large supraciliary processes, long calcars, and dermal-cranial co-ossification. *G. bufona* and *G. weinlandii* have shorter heads, with truncate snouts in profile; the former is smaller than *G. guentheri*, and has odontoids on the lower jaw.

Description

The following description is based on 14 specimens. The body is robust; the maximum snout–vent length is 76.0 mm in males, and 82.0 mm in females. The head is casqued, co-ossified, wider than long, and nearly as wide as the body. The snout is rounded in dorsal view, and is anteroventrally inclined from the nostrils to the jaw in profile; it barely protrudes beyond the margin of jaw. The canthus rostralis is angular, elevated in cross-section, and curved. The loreal region is distinctly concave; the lips are rounded. The top of the head is depressed, owing to dorsal flaring of the lateral margins of the frontoparietals. The interorbital distance is about 160% of the width of the upper eyelid. The internarial area is slightly depressed. The nostrils are protuberant, directed laterally at a point below the anterior terminus of the canthus rostralis and slightly posterior to the anterior margin of the lower lip. The diameter of the eye is about 20% greater than its distance from the nostril, and is about three times its distance from the margin of the jaw. The tympanum is narrowly ovoid in an anterodorsal-posteroventral plane, and is separated from the eye by a distance twice the length of the tympanum. The tympanic annulus is indistinct and tubercular. The supratympanic fold is moderately heavy, and is co-ossified anteriorly. The fold extends posteriorly from the posterior corner of the orbit, obscures the upper edge of the tympanum, and becomes diffuse posterior to the tympanum.

The arm is moderately robust; a row of low subconical ulnar tubercles is present on the ventrolateral edge of forearm. An axillary membrane extends about one-fourth the length of the upper arm. The hand is large. The fingers are long, slender, and unwebbed. The discs on the fingers are large and round; the width of the disc on the third finger is twice the length of the tympanum. The relative lengths of the fingers are I = II < IV < III. The subarticular tubercles are large and round; the supernumerary tubercles are small, subconical, and arranged in a single row on the proximal segment of each digit. The palmar tubercle is low, diffuse, and bifid; the prepollical tubercle is elongately elliptical; nuptial excrescences are absent. The hind limb is long and slender. The tibia length is about 62% of the snout–vent length; the foot length is only about 49% of the snout–vent length. There is a triangular calcar (79%) or large tubercle (21%) on the heel. A row of low subconical tubercles is present on the outer edge of the tarsus; there is no inner tarsal fold. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is small, ovoid, and not visible from above. The toes are long and slender. The relative lengths of the toes are I < II < III < V < IV. The toes are about one-half webbed; the webbing formula is **I**1—(1^+–1½) **II**1½—2**III**(1½–2^+)—(3–3½)**IV**(3–3½)—(1½–2)**V**. The subarticular tubercles are large and round; the supernumerary tubercles are low, round, and in a single row on the proximal segment of each toe.

The skin on the dorsum of the body is granular, with scattered small tubercles; the skin on the head is co-ossified with the underlying dermal elements; the skin on the flanks is granular; the skin in the axilla is areolate; the skin on the belly and posteroventral surfaces of the thighs is coarsely granular; other surfaces are smooth. A conspicuous supraciliary process is elongate and triangular. A row of three or four tubercles diverge posteroventrally from the cloacal opening. The opening of the brood pouch is narrowly V-shaped, with the anterior border at the level of the sacrum. The dentigerous processes of the vomers are posteromedially inclined, and are moderately separated medially behind the level of the ovoid choanae. Each process bears four to seven teeth.

COLOR IN PRESERVATIVE

There are two color patterns. In the first, the dorsum is tan or brown, with darker brown markings consisting of an interorbital chevron, narrow canthal stripe, narrow dorsolateral line, broad ventrolateral stripe, irregular middorsal marks, and flecks. The limbs are tan or brown, with dark brown transverse bars: three or four on the forearms, six or seven on the thighs, and four or five each on the shanks and tarsi. The anterior surfaces of the thighs are tan, with vertical brown bars confluent with those on the dorsal surfaces. The posterior surfaces of the thighs are brown. The margin of the upper jaw is dark brown, interrupted by small cream marks; suborbital bars are absent. The venter is creamy brown. In the second pattern, the dorsum is bluish gray to black, with numerous small red to cream flecks on the dorsum of the head, body, and limbs and on the flanks. The venter is creamy brown. A supracloacal stripe is absent. The anal region is dark brown, with a pair of white subcloacal spots (53%). The outer toes and webbing are darker than the inner ones in all but one specimen.

COLOR IN LIFE

Of 20 adults and various subadults, 10 adults (3 males, 7 females) were tan, with brown markings; 8 (6 males, 2 females) were dark brown to grayish black, with pale flecks; 2 adults (1 male, 1 female) and all juveniles were green, with or without an indistinct brown dorsolateral line or cream flecks on the flanks. The iris is pearly white above, with dark brown triangles (apices positioned medially) anteriorly and posteriorly, and pink to reddish brown below.

The variation in color is documented by the following descriptions of three adults from Quebrada Zapadores, 5 km ESE of Chiriboga, Provincia de Pichincha, Ecuador (W. E. Duellman field notes, 3 April and 11 May 1975).

KU 164224.—The dorsum is sepia umber, with small bright red spots; the flanks are dark brown. The anterior surfaces of the thighs are brown, indistinctly mottled with cream; the posterior and ventral surfaces of the thighs are olive brown. The inner surfaces of the shanks and tarsi are brown, mottled with greenish cream. The chin and pectoral region are greenish gray, with brown and gray mottling and flecks; the abdomen is brown, with a few minute white flecks. The plantar surfaces are brown; the palmar surfaces are olive brown. The anal tubercles are white; the tongue is dull orange; the buccal lining is pale green.

KU 164226 (Fig. 10.30A).—The dorsum (except the thighs) is reddish brown, with dark brown mottling on the back, a chevron-shaped interorbital mark, labial bars, and transverse bars on the limbs. The flanks are a paler reddish brown, with prominent dark brown

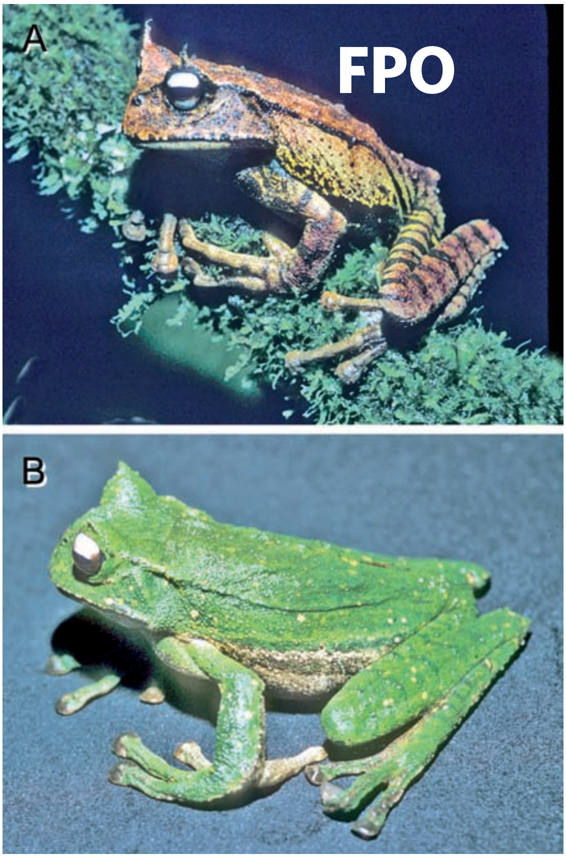

Fig. 10.30 *Gastrotheca guentheri*. A: KU 164226, female, 74.7 mm SVL. B: KU 164228, female, 82.0 mm SVL. Both from Quebrada Zapadores, Provincia de Pichincha, Ecuador. Photos by W. E. Duellman.

marks: from the canthus, along the upper eyelid, and over the tympanum diagonally to the groin, as well as a broad stripe from the axilla to the groin, bordered above by bright deep yellow. The dorsal surfaces of the thighs are reddish brown, with bold dark brown transverse bars extending onto the dull yellow anterior surfaces of the thighs. The posterior and ventral surfaces of the thighs, inner surfaces of the limbs, and palmar and plantar surfaces are dull gray brown. The throat is grayish brown and paler than the abdomen, which has a few minute white flecks.

KU 164228 (Fig. 10.30B).—At night the dorsum is pale emerald green; the belly is pale greenish white. By day the dorsum is darker green, with cream flecks. The labial margin is dark brown. There are cream flecks along the outer margins of the forearms and hind limbs, and cream spots and flecks along the flanks between the dorsal and ventral coloration. The venter is palest on the throat, where it is suffused with brown flecks and blotches that are interspersed with cream flecks; the venter is darkest on the belly, the ventral surfaces of the tarsi, and the plantar surfaces. The tongue and lining of the mouth are ochre.

MCZ 108616 from Quebrada La Plata, Provincia de Pichincha, Ecuador.—This adult male is somewhat different. The dorsum is maroon, with indistinct black mottling. Between the folds of the brood pouch the back is black; behind this it is red. The head is cinnamon colored, mottled with black and maroon; the flanks are yellowish brown, with burnt-umber longitudinal stripes. The thighs are yellowish brown, with burnt-umber bars; other parts of the limbs are chestnut colored, with burnt-umber bars. Some yellowish-green patches are evident below and in front of the eyes. The venter is grayish green, somewhat paler on the throat. The fingers are greenish olive underneath. The tongue and margins of the jaws are bright yellow (K. Miyata field notes, 3 February 1979).

A brown female from La Planada, Departamento de Nariño, Colombia, gave birth to 14 young, all of which were uniformly green (Fig. 10.31) (Duellman and Ruíz-Carranza, 1986).

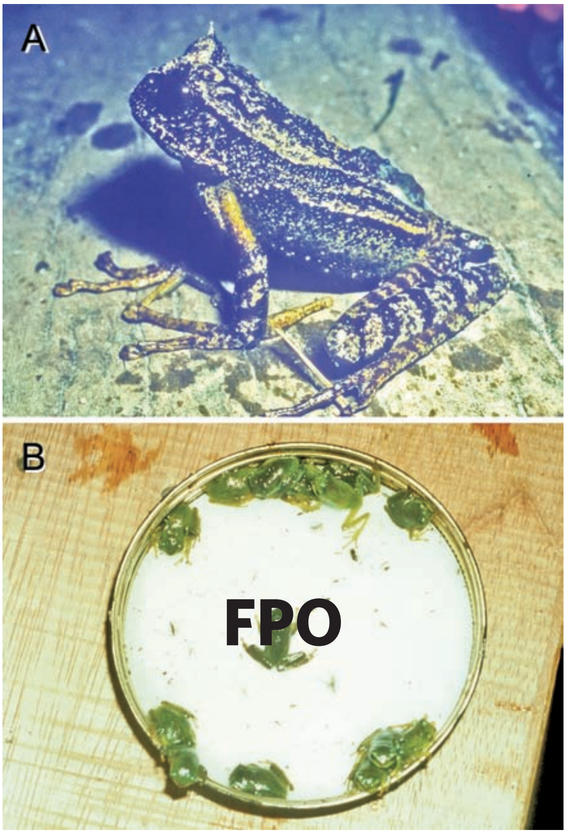

Fig. 10.31 *Gastrotheca guentheri*. A: female from La Planada, Nariño, Colombia. B: recently birthed offspring from the female in A. Photos by P. A. Burrowes, KUDA.

MEASUREMENTS

Significant morphometric differences between the sexes exist in only three measurements: foot length, orbit–jaw distance, and thumb length (Table 10.9).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a heterogeneous fine pit-and-ridge pattern. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange and a moderate-sized otic flange. A temporal arcade is absent. The frontoparietal covers the anterior epiotic eminence and the anterior part of the posterior epiotic eminence. The frontoparietal is not fused to the epiotic eminence; therefore the carotid canal is open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for about half the length of the rostrum. The pars facialis of the maxilla is distinctly separated from the alary process of the premaxilla, and has only a narrow overlap with the dental process of the pre-

Table 10.9 Univariate statistics for adults of *Gastrotheca guentheri*

	Males ($n = 5$)			Females ($n = 9$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	72.9	67.8–76.0	3.10	74.2	69.9–82.0	3.69
Tibia length	45.1	43.1–48.9	2.16	46.6	42.7–48.7	1.83
Foot length**	32.5	37.4–40.5	1.36	39.8	37.4–43.5	2.18
Head length	25.7	24.9–26.3	0.56	26.5	25.2–27.8	0.83
Head width	29.2	28.1–30.2	0.76	31.1	29.9–34.3	1.34
Interorbital distance	9.2	8.8–10.0	0.51	9.9	9.2–10.2	0.36
Eyelid width	5.7	4.7–7.0	0.88	6.1	5.9–6.7	0.39
Internarial distance	4.1	4.0–4.3	0.15	4.4	4.0–5.0	0.35
Eye diameter	7.1	6.5–7.7	0.53	7.7	6.7–9.0	0.88
Eye–nostril distance	6.2	5.8–6.8	0.40	5.7	5.8–6.8	0.19
Orbit–jaw distance**	3.4	3.3–4.6	0.20	4.7	4.2–5.4	0.52
Nostril–jaw distance	5.8	5.1–6.3	0.51	6.7	5.8–8.0	0.75
Tympanum diameter	2.5	2.3–3.7	1.30	2.4	2.1–2.7	0.17
Thumb length**	13.9	15.2–16.5	0.46	16.6	15.2–17.8	0.94
Third finger length	29.4	28.3–30.9	1.15	30.5	28.3–32.0	1.21
Disc width	4.7	4.3–5.1	0.29	5.0	4.6–5.5	0.32

**Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

maxilla. The quadratojugal is short. The postorbital process of the maxilla is massive, and has a broad diagonal articulation with the massive zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the otic plate completely articulates with and broadly overlaps the ossified crista parotica. The relative sizes of the dorsal and ventral parts of the stapedial footplate, when viewed in posterior aspect, could not be determined. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has a blunt terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are narrowly separated medially; each bears a low irregular ventral ridge. The pterygoid does not articulate with the squamosal, and lacks a dorsal ramus on its anterior ramus. The vomers bear moderately large dentigerous processes located between the posterior margins of the choanae. Pedicellate bicuspid teeth are present on the dentary of the mandible.

Life History

Eggs undergo development directly into froglets. Three brooding females contained eggs in the brood pouches. One from La Planada, Departamento de Nariño, Colombia, having a snout–vent length of 71.0 mm, was collected in November and contained 12 embryos in Stage 33; the diameter of the yolk was 11.0 mm. One from Tandapi, Provincia de Pichincha, Ecuador, having a snout–vent length of 82.0 mm, was collected in June and contained 12 embryos in Stage 38; the diameter of the yolk was 11.3 mm. One female from an unknown locality in Ecuador and without date, having a snout–vent length of 72.3 mm, contained 15 embryos in Stage 45; the diameter of the eggs was 13.2 mm.

A brooding female found at La Planada, Colombia, on 1 May 1986 gave birth to 14 young on 28 May 1986 (P. A. Burrowes field notes). Two juveniles having snout–vent lengths of 20.5 and 21.0 mm were found at La Planada in March. These data indicate that the clutch size for this species is small (12–15 eggs). The presence of brooding females in at least May, June, and November suggests that the reproductive season is long, and possibly is continuous throughout the year, in the aseasonal cloud forest.

Advertisement Call

The call consists of a single, loud "bop," usually repeated at intervals of several minutes. Some individuals have been heard to produce two or three calls in quick succession. No recordings are available.

Distribution and Ecology

Gastrotheca guentheri occurs in cloud forest at elevations of 1200–2010 m on the Pacific slopes of the Cordillera Occidental in Colombia and Ecuador; a hiatus of more than 500 km exists in the known range in Colombia. A single specimen purportedly is from an elevation of 2690 m on the Amazonian slopes of the Cordillera

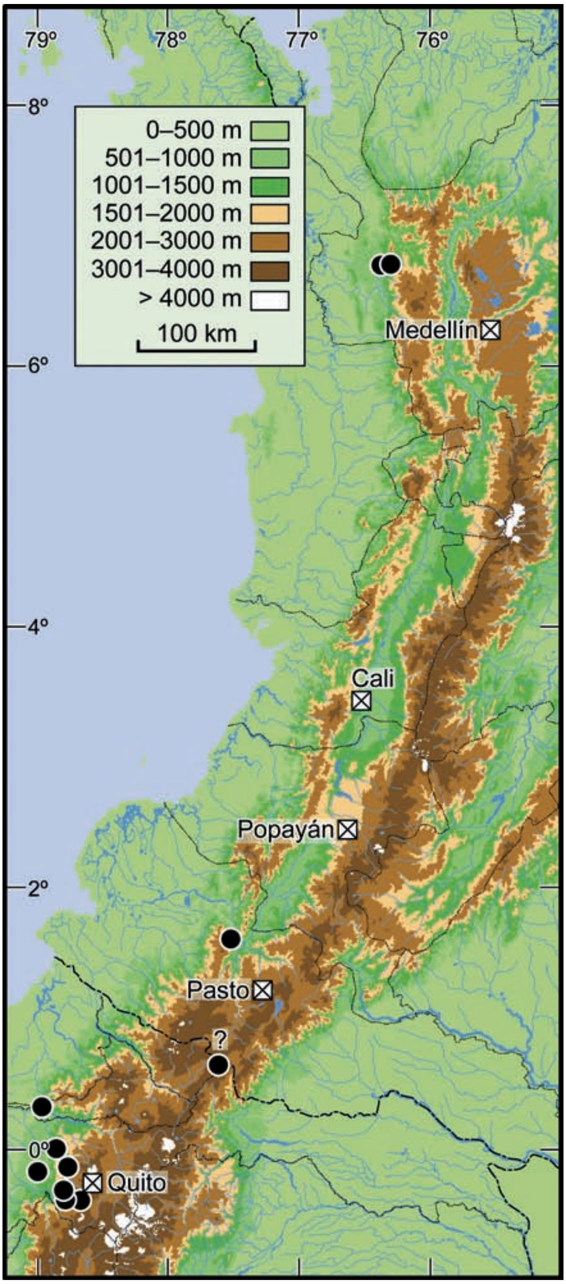

Fig. 10.32 Western Colombia and Ecuador, showing the localities of known occurrences of *Gastrotheca guentheri*.

Oriental in extreme northern Ecuador (Fig. 10.32). At night, most adults have been found at heights of 5–10 m on branches of trees. Juveniles were found 1–2 m above the ground, on leaves of bushes.

Conservation Status

This species is categorized as Vulnerable in the IUCN Red List, which notes that the major threats to the taxon are habitat loss because of agricultural development, logging, human settlement, and pollution resulting from the spraying of illegal crops. A presumed decline in Ecuador is unexplained and has taken place within suitable habitats; the decline might be related either to climate change or to chytridiomycosis.

Etymology

The specific name *guentheri* is a patronym for Albert C. L. G. Günther of the British Museum (Natural History).

Remarks

This species is unique among anurans in having true teeth on the lower jaw. Since its description by Boulenger (1882), *Gastrotheca guentheri* was recognized in the monotypic genus *Amphignathodon*. Duellman et al. (1988) showed that immunologically, *Amphignathodon* was not distinct from other long-legged arboreal *Gastrotheca*, and they suggested that *Amphignathodon* Boulenger, 1882, be considered a junior synonym of *Gastrotheca* Fitzinger, 1843. This placement was confirmed in the phylogenetic analysis of DNA sequences by Wiens et al. (2007). The cranial osteology, external morphology, reproductive biology, and advertisement call also support this placement.

Wiens (2011:1294) used a time-calibrated phylogeny to show "strong support for the re-evolution of lost mandibular teeth in frogs." In his analysis, the most recent common ancestor of frogs and other lissamphibians was 230 million years ago, at which time mandibular teeth were lost in frogs. According to Wiens, these teeth "re-evolved" with the divergence of *Gastrotheca guentheri* and *G. weinlandii* 4.64 million years ago; presumably the developmental constraint against mandibular teeth in frogs was breached in *G. guentheri*.

Although the external structure and coloration distinguish *Gastrotheca guentheri* from other long-legged arboreal *Gastrotheca* on the Pacific versant of South America, all of the species are similar in size and proportions. A stepwise discriminant analysis distinguishes *G. guentheri* on the first canonical axis: head width, interorbital distance, and thumb length (Fig. 10.15).

All known juveniles of *Gastrotheca guentheri* are essentially a uniform green dorsally, a coloration known in only 10% of the adults. As noted by Duellman and Ruíz (1986), ontogenetic polymorphism evidently occurs in this species: some adults develop a pattern of brown streaks; others are dark gray, with red flecks; and some remain green.

Gastrotheca (*Amphignathodon*) *helenae* Dunn

Gastrotheca helenae Dunn, 1944:404.—Holotype: MLS 268 from Páramo de Tamá, Departamento de Norte de Santander, Colombia.

Gastrotheca (*Amphignathodon*) *helenae*—Dubois, 1987:31.

Diagnosis

Adults of this moderately large species attain a snout–vent length of 65.8 mm. The tibia length is about 50% of the snout–vent length, and is slightly longer than the foot. The interorbital region is about twice as wide as the upper eyelid. The skin on the dorsum is smooth or granular, not adherent to or co-ossified with the skull, and lacks transverse ridges. A supraciliary process is absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth or granular. The first and second fingers are equal in length. The discs on the fingers are slightly wider than the digits. The fingers are webbed basally; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is either tan, with brown longitudinal marks, or dark brown to black, with small pale spots. A dark canthal stripe is present; a pale dorsolateral stripe usually is present. The flanks and venter are uniformly dark brown.

The only other species of *Gastrotheca* having a color pattern similar to the morph of *G. helenae* that has longitudinal brown stripes is the Argentinean *G. gracilis*, which is small (snout–vent length to 45 mm), has tuberculate skin on the dorsum, and has the first finger shorter than the second. The color morph of *G. helenae* that is dark brown to black, with pale flecks, is similar to a spotted pattern in *G. aureomaculata*, which differs from *G. helenae* by having a golden tympanum and a narrower interorbital distance.

Description

The following description is based on 12 specimens. The body is robust; the maximum snout–vent length is 65.0 mm in males, and 65.8 mm in females. The head is wider than long, and as wide as the body. The snout is acutely rounded in dorsal view, and is truncate in profile. The canthus rostralis is angular in cross-section, and is curved. The loreal region is slightly concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 200% of the width of the upper eyelid. The internarial area is flat. The nostrils are barely protuberant, and are directed laterally at a point below the anterior terminus of the canthus rostralis. The diameter of the eye is slightly greater than its distance from the nostril and from the margin of the jaw. The tympanum is vertically ovoid, and is separated from the eye by a distance three times the length of the tympanum. The tympanic annulus is indistinct, and is tubercular or smooth. The supratympanic fold is moderately heavy; it obscures the upper edge of the tympanum, and extends from the posterior corner of the eye to a point posterior to the tympanum.

The arm is moderately robust; a row of small conical tubercles is present on the ventrolateral surface of forearm. The hand is large. The fingers are long, and webbed basally; the webbing formula for the outer fingers is **II**2^{+}—3**III**2^{-}—3^{-}**IV**. The discs on the fingers are small, round, and slightly wider than the digits. The width of the disc on the third finger is barely larger than the length of the tympanum. The relative lengths of the fingers are I = II < IV < III. The subarticular tubercles are moderately large and round; the distal tubercles on the third and fourth fingers are bifid. The supernumerary tubercles are small, subconical, and numerous on the proximal segments of the third and fourth fingers. The palmar tubercle is low and bifid; the prepollical tubercle is ovoid, and lacks a nuptial excrescence. The hind limb is moderately robust. The tibia length is about 50% of the snout–vent length; the foot length is about 49% of the snout–vent length. Calcars, tarsal tubercles, and an outer metatarsal tubercle are absent; the inner metatarsal tubercle is small and ovoid. An inner tarsal fold is low, and is curved on the distal one-third of the tarsus. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. The toes are about one-half webbed; the webbing formula is **I**2—2**II**2—2^{-}**III**2—3**IV**3—2^{-}**V**. The subarticular tubercles are small, low, and round; the supernumerary tubercles are small, and are present only on the proximal segments of the toes.

The skin on the dorsum of the head, body, and limbs is smooth to weakly areolate in most individuals, but granular in those having a spotted pattern; the skin on the flanks is areolate; the skin on the belly and proximal posteroventral surfaces of the thighs is granular; other surfaces are smooth. A pair of large tubercles is present below the cloacal opening. The opening of the brood pouch is broadly U-shaped, with the anterior border at the level of the sacrum. The dentigerous processes of the vomers are transverse, and are narrowly separated medially between the posterior margins of the small round choanae. Each process bears four to six teeth.

COLOR IN PRESERVATIVE

Two distinctly different color patterns are known (Duellman and Ruíz, 1986). The color pattern of most specimens consists of a creamy tan to brown dorsum, with darker brown or black longitudinal markings on the body: a middorsal stripe bifurcating posteriorly, and dorsolateral stripes. The flanks are dark brown, bordered above by a narrow cream stripe. The margin of the upper lip is white. A brown or black canthal stripe is continuous across the tip of the snout and down nearly to the margin of the lip. The anterior and posterior surfaces of the thighs are black; the dorsal surfaces of the shanks are cream to brown, with four to six darker brown transverse bars. A creamy white supracloacal stripe and a pair of white subcloacal tubercles is present. The venter is dark brown, with diffuse darker brown spots, and with or without creamy flecks or diffuse mottling on the chest; the vocal sac is dark brown to black. In two adults (ICN 10548 and KU 181070) the dorsum is black, with cream or orange flecks; the venter is cream, with a black throat and a blackish suffusion on the anterior part of the chest.

COLOR IN LIFE

In most individuals the dorsum is lemon yellow, pale tan, or reddish brown, with dark brown markings on the body and limbs (Fig. 10.33A). The upper flanks are chocolate brown, bordered above by a cream stripe; the lower flanks are suffused with yellow. Markings on the shanks and feet are bordered by white. The loreal region is yellow, tan, or lime green. Pale blotches on the dorsum of the body and limbs of two specimens are lime green. The venter is gray; the iris is coppery bronze; the tongue and buccal lining are blue (P. M. Ruíz-C. field notes, April 1981, and color photographs). In ICN 10548 the dorsum is chocolate brown, with deep yellow flecks; the venter is white (from color photographs).

In KU 181070 the dorsum is black, with golden-orange flecks; the venter is black, with white spots (Fig. 10.33B). The iris is dark reddish copper; the tongue and mouth are bluish green (W. E. Duellman field notes, 2 February 1979).

MEASUREMENTS

Females are only slightly larger than males. An ANOVA of measurements of all known adults (eight males, four females) shows that there are no significant differences between the sexes, except for head length ($P \leq 0.01$); all variances are homogeneous, except for the snout–vent length (Table 10.10).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous semicoarse pit-and-ridge pattern. The nasals articulate medially, and are fused to one another, but not to the sphenethmoid posteriorly; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange and a moderately large otic flange. A temporal arcade is incomplete. The frontoparietal covers but is not fused to the anterior epiotic eminence; therefore the carotid canal is open, and posteriorly exits the skull adjacent to the posterior epiotic

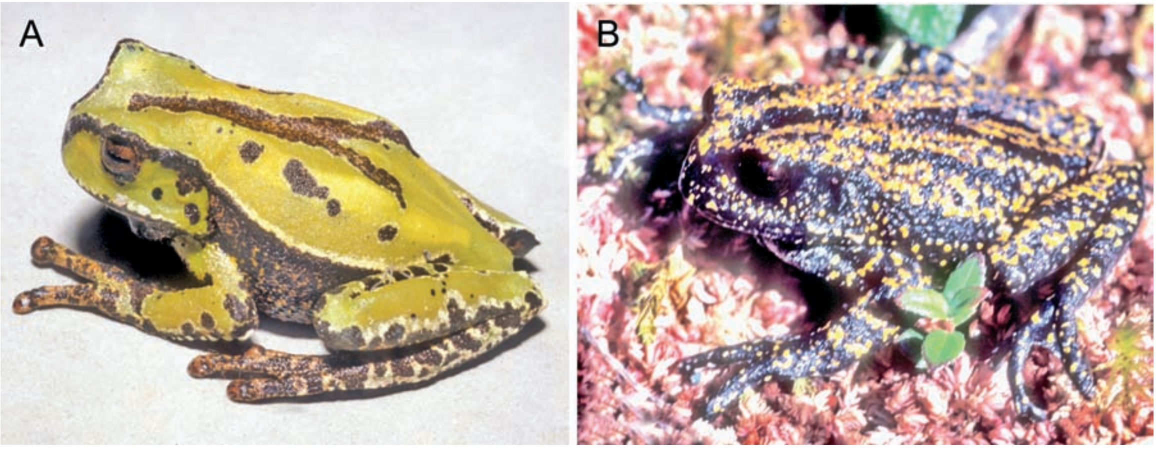

Fig. 10.33 *Gastrotheca helenae*. A: ICN 10545, male, 65 mm, Cerro Tamá, Norte de Santander, Colombia. B: KU 181070, male, 51 mm SVL, Cerro Tamá, Táchira, Venezuela. Photos by P. M. Ruíz-C. (A) and W. E. Duellman (B), KUDA.

Table 10.10 Univariate statistics for adults of *Gastrotheca helenae*

	Males ($n = 8$)			Females ($n = 4$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	60.5	51.0–65.8	5.25†	63.8	62.5–65.0	1.33
Tibia length	30.9	23.3–34.5	3.54	32.5	31.0–34.8	1.61
Foot length	29.5	25.3–33.5	3.10	31.7	27.0–33.8	3.13
Head length**	20.0	18.0–21.8	1.28	22.2	21.5–23.5	0.94
Head width	23.3	20.0–26.1	1.96	25.0	24.5–26.6	1.05
Interorbital distance	8.8	6.6–9.5	1.06	9.0	8.5–9.3	0.36
Eyelid width	4.6	3.0–5.8	0.88	4.6	4.5–5.0	0.25
Internarial distance	4.1	3.1–4.7	0.61	3.9	3.5–4.7	0.57
Eye diameter	6.3	4.6–7.0	0.77	6.6	6.0–7.5	0.68
Eye–nostril distance	5.2	4.3–6.0	0.57	5.5	5.0–5.8	0.36
Orbit–jaw distance	4.6	3.3–5.4	0.68	5.1	4.9–5.3	0.17
Nostril–jaw distance	5.3	4.0–5.8	0.62	5.9	5.5–6.1	0.27
Tympanum diameter	2.9	1.8–3.4	0.51	3.2	2.6–4.0	0.65
Thumb length	12.6	11.3–13.8	0.89	13.6	12.2–15.0	1.17
Third finger length	21.6	18.8–23.8	1.70	23.2	21.6–25.0	1.41
Disc width	3.7	2.7–4.1	0.46	3.8	3.1–5.0	0.85

**Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

†Variances are non-homogeneous (Levene's test for equal variances, $P \leq 0.05$).

eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which has a short (< 25% of the length of the rostrum) articulation with the nasal. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The postorbital process of the maxilla is massive, and has a broad horizontal articulation with the massive zygomatic process of the squamosal. The head of the squamosal bears a wide crest; the otic plate completely articulates with and moderately overlaps the ossified crista parotica. The dorsal part of the stapedial footplate is between two and three times the length of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has a blunt terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, where it is separated from the prootic by cartilage. The neopalatines are moderately separated medially; each bears a low irregular ventral ridge. The pterygoid articulates with the medial surfaces of both the postorbital process of the maxilla and the zygomatic ramus of the squamosal via a broad low dorsal expansion of the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located at the posterior margins of the choanae.

Life History

The eggs hatch into froglets. The holotype is a female having a snout–vent length of 62.5 mm, containing 12 partly developed embryos in the pouch; it was collected on 27 October 1941. A female having a snout–vent length of 64.9 mm, obtained on 27 April 1981, gave birth to 12 young having snout–vent lengths of 20.0–22.2 mm ($\bar{x} = 21.0$). The female (ICN 10548) was dark brown, with pale flecks. All of the young were pale creamy tan, with dark brown markings consisting of a middorsal stripe bifurcating posteriorly around the pouch area, dorsolateral stripe, and flanks bordered above by a narrow white line; the venter was yellow, with brown flecks (Fig. 10.34).

Advertisement Call

According to the field notes of Pedro M. Ruíz-C., the call consists of 12–15 monosyllabic notes in a period of about 5 seconds; the call is repeated every 20–30 minutes.

Distribution and Ecology

This species is known only from Cerro Tamá in the Cordillera Oriental on the Colombian-Venezuelan

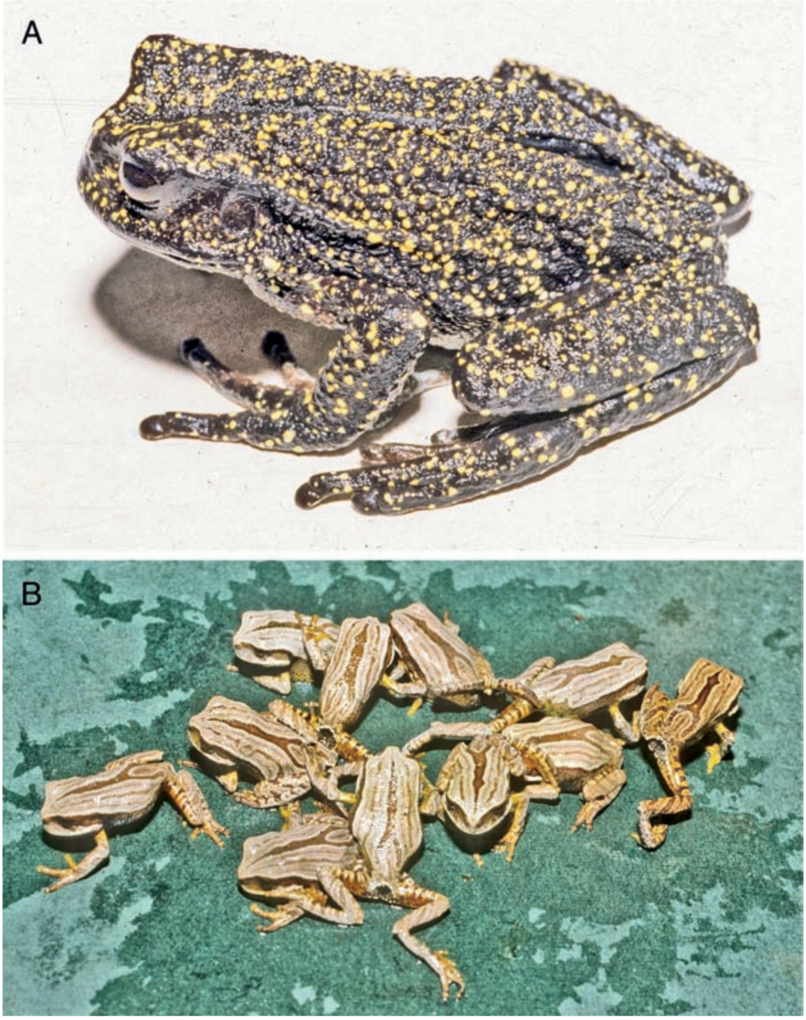

Fig. 10.34 *Gastrotheca helenae*. A: ICN 10548, female, 64.9 mm SVL, with a dark brown dorsum and yellow flecks. B: newly born young from ICN 10548. Note that all have a different color pattern than their mother. Photos by P. M. Ruíz-C., KUDA.

border (Fig. 10.35). The holotype, obtained in October 1941, is from the Páramo de Tamá, which could be at any elevation above 3000 m. On 3 February 1979, I obtained one individual at 3250 m on the northeastern slope (Venezuelan side) of Cerro Tamá. The frog was buried in sphagnum moss in subpáramo by day. On 23–24 April 1981, Pedro M. Ruíz-C. collected 10 adults in the Parque Nacional Natural Tamá on the northwestern slope (Colombian side) of Cerro Tamá. One female was on the ground, in subpáramo at an elevation of 2800 m, whereas all of the others were taken in forest at 2300 m. By day one was in a terrestrial bromeliad, and one was under the fronds of a tree fern. At night, one was 1 m above the ground in a shrub, and the others were on the ground. More recently, 70 individuals were reported from five localities, at elevations of 2700–3200 m on the Colombian slopes of Cerro Tamá (Acevedo et al., 2011). The frogs were most abundant in the páramo at 3200 m, where individuals were found in moss by day; males called at temperatures of 6°C–8°C at 2000–0100 hours and also at 0600–0800 hours.

Conservation Status

Acevedo et al. (2011) recommended that this species should be categorized as Data Deficient in the IUCN Red List. The majority of localities from which the taxon are known are within the Parque Nacional Natural Tamá in Colombia. Even so, the species may be threatened by fires in the páramo and grazing by cattle at lower elevations.

Etymology

The specific name *helenae* is a patronym for Helen T. Gaige, who worked on *Gastrotheca* early in the twentieth century.

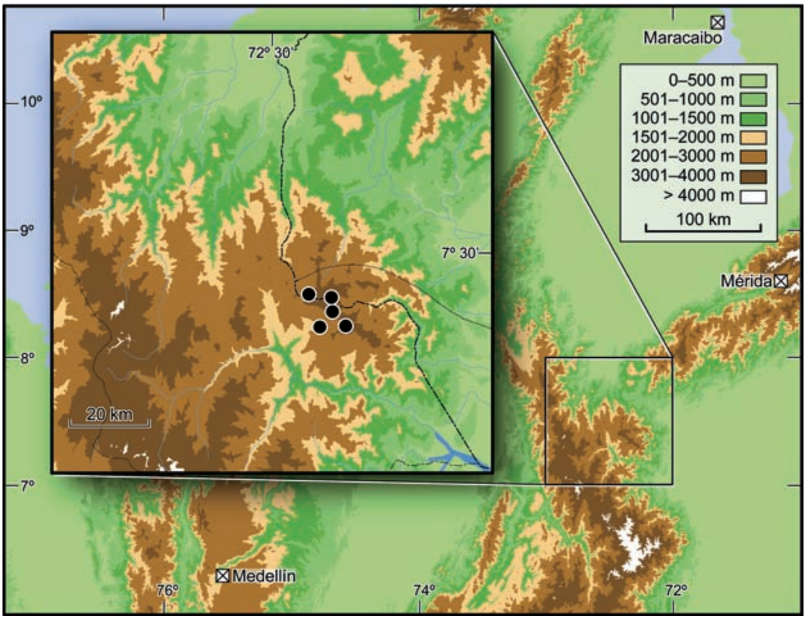

Fig. 10.35 Vicinity of Cerro Tamá on the Colombia-Venezuela border, showing the localities of known occurrences of *Gastrotheca helenae*.

Remarks

The two distinctive color patterns of *Gastrotheca helenae* are correlated with skin texture. The two adults that are black, with pale flecks, have granular skin on the dorsum; those that are pale, with dark longitudinal markings, have smooth or finely areolate skin on the dorsum. These distinctive patterns and skin textures do not represent specific differences, because one black female with pale flecks (ICN 10548) gave birth to 12 young, all of which were pale, with dark longitudinal stripes.

One individual (KU 181070) was accidentally kicked out of deep sphagnum moss at an elevation of 3250 on Cerro Tamá. The frog would have been overlooked had it not opened its mouth, thereby displaying the bright bluish-green tongue and buccal lining, and emitted a loud buzz-like distress call.

Gastrotheca (*Amphignathodon*) *longipes* (Boulenger)

Nototrema longipes Boulenger, 1882:418.—Syntypes: BMNH 1947.1.31.4 from Canelos and 1947.2.31.5 from Sarayacu, Provincia de Pastaza, Ecuador.

Hyla capitocarinata Andersson, 1945:75.—NHRM 1959 from the Río Pastaza watershed, Ecuador. Synonymy fide Duellman, 1974:2.

Gastrotheca longipes—Peters, 1955:343.

Gastrotheca longipes—Duellman, 1974:2.

Gastrotheca (*Amphignathodon*) *longipes*—Dubois, 1987:31.

Diagnosis

This large species attains a snout–vent length of 88.3 mm. The tibia length is more than 50% of the snout–vent length, and is slightly longer than the foot. The interorbital distance is only slightly greater than the width of the upper eyelid. The skin on the dorsum is smooth, not adherent to or co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is granular. The first and second fingers are equal in length. The discs on the fingers are much wider than the digits proximal to the discs. The fingers are about one-fourth webbed; on the foot the webbing extends maximally to a point midway between the penultimate and distal subarticular tubercles on the fourth toe and the distal subarticular tubercle on the fifth toe. The dorsum is green, with or without dark or white spots. Markings on the head consist of a dark interocular bar, and a dark canthal stripe or not. A pale dorsolateral stripe is absent. The flanks are uniformly green; the venter is uniformly cream.

Gastrotheca longipes most closely resembles *G. andaquiensis*, *microdiscus*, and *albolineata*. The former differs by having a proportionately longer tibia (greater than 60% of the snout–vent length), finely granular skin on the dorsum, a supraciliary process, an elongate calcar, and dark mottling on the dorsum. *G. microdisca* differs from *G. longipes* by having a proportionately wider interorbital distance (170%–200% of the eyelid width); first finger longer than the second; unwebbed fingers; and tan or brown flanks, with or without dark markings. The smaller (snout–vent length to 60 mm) *G. albolineata* differs by having a tibia length less than 50% of the snout–vent length, first finger longer than the second, outer fingers more than one-half webbed, a pale labial stripe, and a broad pale dorsolateral stripe. *G. orophylax* and *G. carinaceps* also are uniformly green; both have a proportionately wider interorbital distance (about 200% of the eyelid width) and unwebbed fingers. *G. orophylax* also differs by having a truncate snout in profile, and *G. carinaceps* differs by having prominent cranial crests.

Description

The following description is based on 25 specimens. The body is robust; the maximum snout–vent length is 70.8 mm in males, and 88.3 mm in females. The head is casqued, but the skin on the head is not adherent to or co-ossified with the skull. The head is slightly wider than long, and about as wide as the body. The snout is rounded in dorsal view; in profile, it is abruptly inclined from the nostrils to the tip. The canthus rostralis is angular in cross-section. The loreal region is slightly concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 125% of the width of the upper eyelid. The internarial area is flat. The nostrils are protuberant, and are directed laterally at the terminus of the canthus rostralis at a point posterior to the anterior margin of the lower lip. The diameter of the eye is slightly greater than its distance from the nostril. The tympanum is vertically elliptical, and is separated from the eye by a distance about 1.5 times the length of the tympanum. The tympanic annulus is indistinct and granular. The supratympanic fold is moderately heavy; it extends from the posterior corner of the orbit to the flank, and obscures the upper edge of the tympanum.

The arm is moderately robust, and bears as many as four low ulnar tubercles. The hand is large. The fingers are long, and have large round discs; the width of the disc on the third finger is greater than the length of the tympanum. The relative lengths of the fingers are I ≥ II < IV < III. The fingers are about one-fourth webbed; the webbing formula is **II**(2–2½)—(3–3^{+})**III**(3^{-}–3)—(2^{+}–2½)**IV**. The subarticular tubercles are large and round; none are bifid. The supernumerary tubercles are large and round; they are present only on the proximal segments. The palmar tubercle is small and round; the prepollical tubercle is elongately elliptical; the thumb bears a brown nuptial excrescence in breeding males. The hind limb is moderately slender. The tibia length is about 56% of the snout–vent length; the foot length is about 48% of the snout–vent length. The heel has small tubercles (20%) or a small triangular calcar (80%). The outer edge of the tarsus has a row of low round tubercles. The inner tarsal fold is weakly present on the distal one-third of the tarsus. The outer metatarsal tubercle is low and diffuse; the inner metatarsal tubercle is elliptical, and is visible from above. The toes are long. The relative lengths of the toes are I < II < III = V < IV. The toes are about three-fourths webbed; the webbing formula is **I**1—(2^{-}–2)**II**1—(1–2)**III**1—(1½–2^{-}) **IV**(1½–3^{-})—(1–1½)**V**. The subarticular tubercles are large and round; the supernumerary tubercles are low, round, and present only on the proximal segments.

The skin on the dorsum is smooth; the skin on the flanks is weakly granular; the skin on the belly is coarsely granular. Small tubercles are present in the temporal region. Vertical folds are present lateral to the cloacal opening. The brood pouch is V-shaped, with the anterior margin at the level of the sacrum. The dentigerous processes of the vomers are transverse, and are narrowly separated medially at the level of the anterior margins of the choanae. Each process bears six to nine teeth.

COLOR IN PRESERVATIVE

The dorsum is pale gray to cream, usually with small dark brown spots (68%) or flecks (28%) on the dorsum, a brown interorbital bar (80%), and a dark brown patch in the cloacal region (92%). The dorsal surfaces of the thighs rarely (8%) have dark spots. A pale labial stripe usually (84%) is absent; a dark brown canthal stripe is present (44%) or absent (56%). The flanks and anterior and posterior surfaces of the thighs are uniformly cream; the outer two toes and intervening web are dark brown.

COLOR IN LIFE

In many individuals the dorsum is nearly a uniform green (Fig. 10.36A); the venter is green or cream.

A juvenile (FSM 42834) from 3.1 km S of Río Tiputini, Provincia de Orellana, Ecuador.—The dorsum and flanks are green, with small white spots that are most numerous on the flanks. There are diffuse brown spots above the eye, and three white spots bordered by brown between the eyes. The supratympanic ridge is white and brown; three white spots, bordered by brown, are present on the anterior part of the body. The limbs are green, with white spots; the upper lip is white; the lower lip is green. The throat and chest are creamy yellow; the belly is green, with creamy yellow spots; the ventral surfaces of the limbs are green. The limb bones also are green. The cloaca is bordered above by white and brown stripes, and laterally by white spots. There are brown spots on the knee; the outer edge of the heel to the tip of the outer toe is white, bordered by brown. There is a white spot below the eye, and another spot at the posterior edge of the jaw; the iris is white, with brown reticulations (M. L. Crump field notes, 8 July 1978).

USNM 258905 from Caterpiza, Región de Amazonas, Peru.—This adult had a green dorsum, with cream labial, ulnar, tarsal, heel, and supracloacal stripes (Fig. 10.36A). There is a dorsolateral row of small white spots on the body, and a diagonal row of small white spots below the orbit. There also is a narrow interrupted white supratympanic stripe. The throat is pale green; the chest is pale yellow. The two outer toes and intervening web are brown; the iris is cream, with brown reticulations (color photos by R. M. McDiarmid, 7 February 1980).

Some individuals (e.g., CORBIDI 11411) have a brown interorbital bar, and brown spots on the dorsum (Fig. 10.36B).

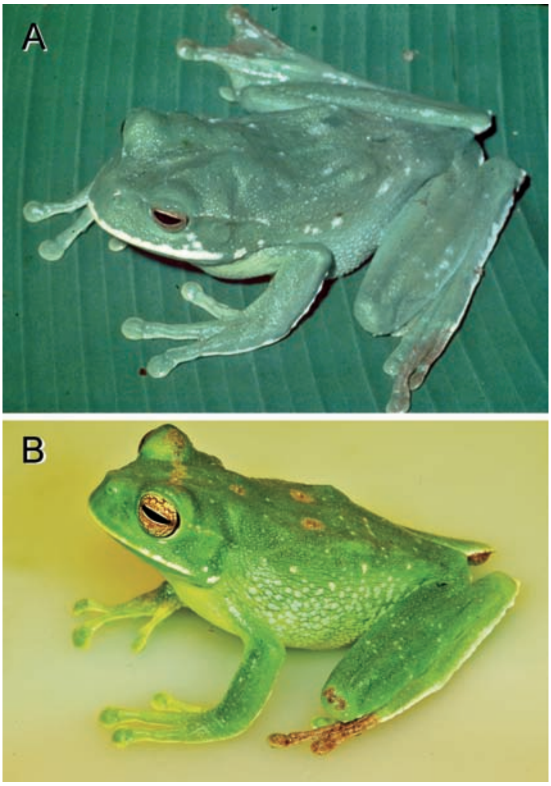

Fig. 10.36 *Gastrotheca longipes*. A: USNM 258905, female, 87.7 mm SVL, Río Caterpiza, Amazonas, Peru. B: CORBIDI 11411, male, 53.7 mm SVL, Ponga Chinim, Amazonas, Peru. Photos by R. W. McDiarmid (A) and A. Catenazzi (B), KUDA.

MEASUREMENTS

Females are significantly larger than males in most measurements, but only two adult males are available for examination (Table 10.11).

CRANIAL OSTEOLOGY

The sphenethmoid is sculptured in an internal vermiform pattern; the remainder of the skull table is smooth. The nasals do not articulate medially, and

Table 10.11 Univariate statistics for adults of *Gastrotheca longipes*

	Males (n = 2)			Females (n = 15)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length**	66.0	61.2–70.8	6.78	80.0	70.0–88.3	6.48
Tibia length**	37.5	35.5–39.4	2.76	49.1	44.3–52.9	2.77
Foot length**	29.4	27.8–30.9	2.19	38.1	33.3–41.7	2.32
Head length**	21.2	20.8–21.5	0.50	28.0	24.2–31.7	2.53
Head width**	23.6	22.8–24.4	1.13	31.2	27.7–35.3	2.47
Interorbital distance*	7.5	7.4–7.6	0.14	9.0	7.5–10.9	0.84
Eyelid width	5.4	4.7–6.1	0.99	6.4	4.5–7.5	0.95
Internarial distance	4.5	4.1–4.8	0.50	5.4	4.2–6.4	0.68
Eye diameter	6.8	6.3–7.2	0.64	7.5	6.5–8.7	0.74
Eye–nostril distance**	5.8	5.6–5.9	0.21	6.9	5.5–7.6	0.53
Orbit–jaw distance**	3.4	3.3–3.5	0.14	4.6	3.7–5.3	0.51†
Nostril–jaw distance*	4.9	4.8–5.0	0.14	6.2	4.8–7.3	0.70
Tympanum diameter	3.7	3.5–3.9	0.28	3.8	2.8–5.4	0.68
Thumb length**	14.0	13.7–14.3	0.42	17.6	15.3–19.2	1.24
Third finger length**	22.2	21.0–23.3	1.62	29.3	25.3–31.9	2.09
Disc width	4.2	3.9–4.5	0.42	5.2	4.0–6.0	0.54

*Differences between the means of the sexes are significant (ANOVA, $P = 0.05$).

**Differences between the means of the sexes are significant (ANOVA, $P \le 0.01$).

have a simple articulation with the sphenethmoid posteriorly; posterolaterally, the nasal does not articulate with the frontoparietal. The frontoparietals have a complete articulation medially. The supraorbital flange is narrow; the otic flange is absent. A temporal arcade is absent. The frontoparietal does not cover the epiotic eminences; therefore the carotid canal is open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a distinct angle between 31° and 45°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which has a long (>75% of the length of the rostrum) articulation with the nasal. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The postorbital process of the maxilla is present, and has a tenuous articulation with the slender zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the otic plate completely articulates with and moderately overlaps the ossified crista parotica. The dorsal part of the stapedial footplate is between two and three times the length of the ventral part, when viewed in posterior aspect. The relative sizes of the dorsal and ventral parts of the stapedial footplate are about equal, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified posterior to the midlength of the orbit, but is not synostosed with the prootic. The neopalatines are widely separated medially; each bears a flange-like ventral ridge. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via an acuminate recurved dorsal ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located at the posterior quadrants of the choanae.

Life History

One female (CAS 149429) contained 17 eggs, having diameters of up to 10.9 mm, in the brood pouch. Another female (EPN 2732), having a snout–vent length of 78.3 mm, contained 15 embryos in the brood pouch (Almendáriz and Cisneros-Heredia, 2005). The small number of large eggs indicates that the eggs undergo direct development into froglets.

Advertisement Call

The call is unknown.

Distribution and Ecology

Gastrotheca longipes has a rather limited distribution: in the upper Amazon Basin, and on the lower slopes of the Andes (< 500 m) in southern Ecuador and extreme northern Peru (Fig. 10.37). Individuals have been found at night on branches of bushes and trees in lowland tropical rainforest.

Etymology

The specific name is derived from the Latin words *longus* and *pes*, meaning "long" and "foot," respectively. The name refers to the long foot of this species.

Remarks

Duellman (1974) provided details on the type specimens of the nominal species, justified the synonymy of *Hyla capitocarinata* Andersson, 1945, with *Nototrema longipes* Boulenger, 1882, and showed that Goin's (1964) placement of *Gastrotheca viridis* Lutz and Lutz, 1939, in the synonymy of *Nototrema longipes* was erroneous. Almendáriz and Cisneros-Heredia (2005) suggested that sexual dichromatism exists in this species. Based solely on two specimens of each sex, they stated that a brown interorbital bar and brown spots were present in males, whereas females were uniformly green.

Gastrotheca (*Amphignathodon*) *weinlandii* Steindachner

Nototrema weinlandii Steindachner, 1892:837.—Holotype: NMW 16481 from "Ecuador."
Hyla pusilla Melin, 1941:48.—Holotype: NHMG 472 from Roque, Región de San Martín, Peru. Synonymy fide Duellman (1974:5).
Gastrotheca weinlandii—Peters, 1955:340.
Gastrotheca weinlandii—Duellman, 1974:5.
Gastrotheca (*Amphignathodon*) *weinlandii*—Dubois, 1987:31.

Diagnosis

This large species attains a maximum snout–vent length of 86.0 mm. The tibia length is greater than 60% of the snout–vent length, and is much longer than the foot. The interorbital distance is noticeably greater than the width of the upper eyelid. The skin on the dorsum is weakly granular, co-ossified with skull, and lacks transverse ridges. Supraciliary processes usually are absent. The heel bears a triangular calcar. The tympanic annulus is granular. The first finger is longer than the second. The discs on the fingers are much wider than the digits proximal to the discs. The fingers are webbed basally; on the foot the webbing extends maximally to a point midway between the antepenultimate

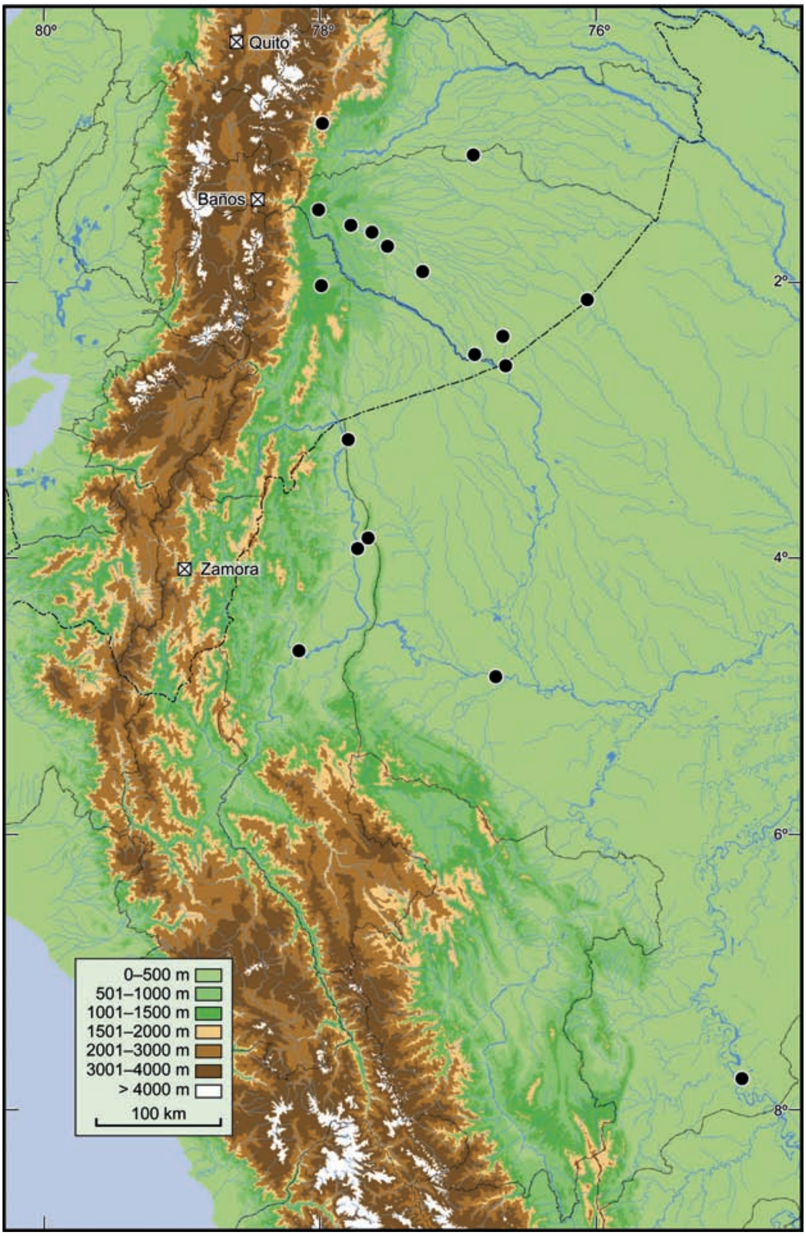

Fig. 10.37 Cordillera Oriental and upper Amazon Basin in Ecuador and Peru, showing the localities of known occurrences of *Gastrotheca longipes*.

and penultimate subarticular tubercles on the fourth toe and to a point midway between the penultimate and distal subarticular tubercles on the fifth toe. The dorsum is tan, with brown chevrons. Markings on the head consist of a narrow U-shaped interocular bar. A pale dorsolateral stripe is absent. The flanks are tan, with diagonal dark marks; the venter is cream, with brown spots.

Seven other species of *Gastrotheca* in northwestern South America have casqued co-ossified heads. Of these, *G. ovifera* differs by having projections on the occipital ridge; a pale dorsum, with a large dark mid-dorsal mark; and uniformly dark flanks. Seven other Andean species are smaller than *G. weinlandii*. In *G. galeata*, the maxillae and premaxillae are flared, so the head has a spatulate appearance. *G. trachyceps* lacks a transverse occipital ridge and has a pale labial stripe, blue groin and hidden surfaces of the thighs, and the first and second fingers about equal in length. *G. bufona* and *G. guentheri* have long supraciliary processes, and the first and second fingers equal in length; *G. antomia* differs from *G. weinlandii* by lacking an occipital ridge, and by having the first finger shorter than the second. *G. nicefori* is like *G. weinlandii* in having an extensively casqued skull with a transverse occipital ridge, but it differs by having the first finger only slightly longer than the second, the snout rounded in profile, a pale dorsum, and dark flanks. The only casque-headed species that approach *G. weinlandii* in size are the Brazilian *G. fissipes* and related members of the subgenus *Eotheca*, all of which have snouts shaped like that in *G. weinlandii*, and also have the first finger much longer than the second.

Description

The following description is based on 15 specimens. The body is robust; the maximum snout–vent length is 75.7 mm in males, and 86.0 mm in females. The head is casqued; the dermal roofing bones are co-ossified with the overlying skin. The head is much wide than long, and as wide as the body. The head width is about 42% of the snout–vent length; the head length is about 35% of the snout–vent length. The snout is broadly rounded, with a truncate tip, in dorsal view; in profile it is slightly inclined anteroventrally, and is nearly truncate. The canthus rostralis is elevated, and is angular in cross-section. The loreal region is concave; the lips are rounded. The top of the head is depressed. The interorbital distance is about 150% of the width of the upper eyelid. The internarial area is flat. The nostrils are slightly protuberant, and are directed anterolaterally below the anterior terminus of the canthus rostralis at a point slightly posterior to the anterior margin of the lower jaw. The diameter of the eye is 25% greater than its distance from the nostril. The tympanum is vertically ovoid, with an anterodorsal-posteroventral axis, and is separated from the eye by a distance about twice the length of the tympanum. The tympanic annulus is indistinct and tubercular. The supratympanic fold is incorporated in a laterally projecting temporal shelf, and obscures the upper edge of the tympanum; the fleshy part of the fold curves posteroventrally to a point above the angle of the jaw.

The arm is moderately robust, and lacks ulnar tubercles. The hand is large. The fingers are long, and bear large round discs; the width of the disc on the third finger is much greater than the length of the tympanum. The relative lengths of the fingers are I > II < IV < III. The fingers have basal webbing and prominent lateral fringes. The subarticular tubercles are moderately large and round; none are bifid; the supernumerary tubercles are small, low, and present only on the proximal segments of the fingers. The palmar tubercle is diffuse and bifid. The prepollical tubercle is elongately elliptical; nuptial excrescences are not evident. The hind limb is slender. The tibia length is about 62% of the snout–vent length; the foot length is about 51% of the snout–vent length. The heel bears a large triangular calcar. Tarsal tubercles are absent. An inner tarsal fold is low but distinct on the distal one-fourth of the tarsus. The outer metatarsal tubercle is small and subconical; the inner metatarsal tubercle is moderately small, elliptical, and visible from above. The toes are long. The relative lengths of the toes are I < II < III = V < IV. The toes are about two-fifths webbed; the webbing formula is **I**2—(2^-–2^+)**II**(1½–2)—(3^-–3) **III**(2–2^+)—(2½–3)**IV**(2½–3)–(1½–2^+)**V**. The subarticular tubercles are small and round; the supernumerary tubercles are low, diffuse, and present only on the proximal segments of the toes.

The skin on the head is completely co-ossified with the underlying dermal elements of the skull; the skin on the dorsum is weakly granular (80%), smooth (14%), or areolate (6%); the skin on the flanks and in the temporal region is granular; the skin on the belly and posteroventral surfaces of the thighs is coarsely granular; other surfaces are smooth. A transverse occipital ridge is present. The temporal region is expanded laterally into a shelf that extends from the posterior corner of the orbit to a point above the angle of the jaw. A small triangular supraciliary process usually (87%) is absent on the margin of the upper eyelid. A pair of tubercles is present below the cloacal opening. The opening of the brood pouch is V-shaped, with the anterior terminus at the level of the sacrum. The vocal sac is very large, median, and subgular. The dentigerous processes of the vomers are posteromedially inclined, and are narrowly separated medially between the posterior margins of the choanae. Each process bears 6–10 teeth.

COLOR IN PRESERVATIVE

The dorsum is tan to brown, with darker brown markings consisting of a narrow and broadly U-shaped interocular mark (absent in 13%), a narrow middorsal mark from the occiput to the sacrum, with posterolateral diagonal marks extending from the middorsal mark onto the flanks (87%), and numerous transverse bars on the limbs (five to seven on each thigh, shank, and tarsus, and three or four on each forearm). The posterior surfaces of the thighs are uniformly brown; the anterior surfaces of the thighs are tan, usually (93%) with dark brown bars. The venter is cream, either with dark spots (86%) or flecks (7%) or uniformly brown (7%). The outer two toes and intervening webbing usually (86%) are darker than the inner ones. A dark patch in the cloacal region and pale spots below the vent are present in 86% of the specimens, but a pale transverse stripe above the vent usually (73%) is absent.

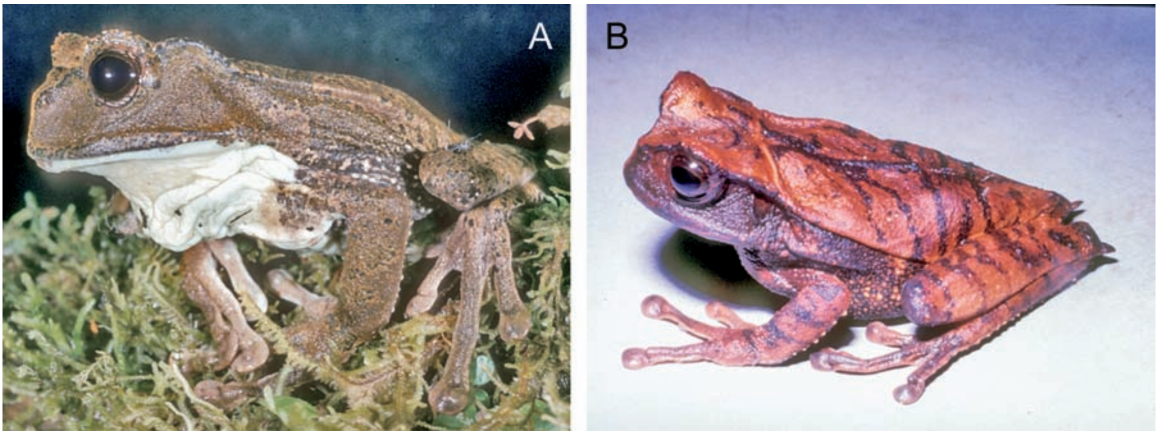

Fig. 10.38 *Gastrotheca weinlandii*. A: KU 143104, male, 85.7 mm SVL, 16.5 km NNE Santa Rosa, Napo, Ecuador. B: ICN 24449, female, 76.7 mm SVL, 12.5 km E Alto de Gabinete, Caquetá, Colombia. Photos by W. E. Duellman (A) and J. D. Lynch (B), KUDA.

COLOR IN LIFE

Although the basic color pattern in living individuals is the same as those specimens in preservative, considerable variation in coloration obtains in adults and juveniles (frontispiece; Fig. 10.38), as is evident from the following descriptions of coloration in life.

KU 122600, from the Cordillera del Dué, Provincia de Sucumbios, Ecuador.—The dorsum is tan, with olive-brown markings. The flanks are dark brown, with yellow flecks. The upper lip and snout are pale yellow; the side of the head is olive green, and is darkest anteriorly. The throat is white; the belly is cream. The iris is reddish bronze, with brown reticulations (W. E. Duellman field notes, 3 August 1968).

KU 143104–05 from 16.5 km NNE Santa Rosa, Provincia de Napo, Ecuador.—The dorsum is either brown, with dark brown markings (KU 143104), or grayish tan, with brown markings (KU 143105). The side of the head is dark brown; the flanks are dark brown, with creamy tan flecks. The ventral surfaces of the limbs are bluish white, with brown markings. The vocal sac and belly are pale green, with brown spots on the belly. The iris is brown; the tongue and buccal lining are blue (W. E. Duellman field notes, 19 October 1971).

KU 146042 from Río Piúntza, Provincia de Morona-Santiago, Ecuador.—The dorsum is grayish green, flecked and marked with brown. The venter is mottled green and brown. There is green on the chin and brown on the ventral surfaces of the limbs; a dark brown dorsolateral stripe to midbody; and yellowish green on the head. The forearms are mottled with brown. The iris is bronze, with brown veins (J. E. Simmons field notes, 6 January 1972).

A juvenile (KU 146041) from Río Piúntza, Provincia de Morona-Santiago, Ecuador.—The dorsum is green. The head is flecked with brown; there is a brown dorsolateral stripe extending to midbody. The venter is translucent yellowish green (J. E. Simmons field notes, 6 January 1972).

A juvenile (KU 202702) from 8.8 km WSW Plan de Milagro, Provincia de Morona-Santiago, Ecuador.—The dorsum is olive tan, with brown markings, including canthal and dorsolateral stripes. The face is pale lime green. The chin is white; the rest of the venter is yellow. The iris is coppery bronze, with fine black reticulations (W. E. Duellman field notes, 4 March, 1984).

MEASUREMENTS

Females are slightly larger than males (Table 10.12).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a heterogeneous fine pit-and-ridge pattern. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange, but lacks an otic flange. A temporal arcade is absent. The frontoparietal covers the anterior epiotic eminence and the anterior part of the posterior epiotic eminence, and is partially fused to them; hence the carotid canal is partially closed, and exits the skull posteriorly adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a mod-

Table 10.12 Univariate statistics for adults of *Gastrotheca weinlandii*

	Males ($n = 6$)			Females ($n = 6$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	74.2	63.0–85.7	8.11	77.9	68.4–86.0	7.71
Tibia length	46.7	39.7–50.5	4.40	47.6	39.9–51.8	5.38
Foot length	38.3	32.6–44.1	4.45	39.2	32.6–42.9	4.33
Head length	26.5	23.4–29.4	2.22	27.4	23.2–30.8	3.19
Head width	31.2	26.9–35.4	3.12	32.3	25.8–35.9	4.77
Interorbital distance	9.9	8.5–11.1	0.98	10.1	7.5–12.7	2.07
Eyelid width	6.4	5.0–7.3	0.83	6.5	4.8–7.8	1.16
Internarial distance	4.5	3.4–5.2	0.64	4.3	3.0–5.1	0.75
Eye diameter	7.6	6.7–8.3	0.64	8.1	6.2–9.9	1.43
Eye–nostril distance	6.4	5.2–7.6	0.92	6.2	5.3–7.0	0.61
Orbit–jaw distance	4.5	3.0–6.2	1.06	4.8	3.9–6.2	0.84
Nostril–jaw distance	6.4	5.2–7.4	0.85	6.2	4.8–6.9	0.77
Tympanum diameter	3.6	3.0–5.7	0.42	4.0	3.0–5.7	1.07†
Thumb length	15.7	12.4–18.2	2.06	16.5	14.0–18.4	1.92
Third finger length	28.5	24.8–31.0	2.37	29.3	24.9–33.9	3.60
Disc width	4.8	3.8–5.4	0.61	4.5	3.9–5.5	0.62

†Variances are non-homogeneous (Brown-Forsythe test, $P \leq 0.05$).

erate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for about half the length of the rostrum. The pars facialis of the maxilla is distinctly separated from the alary process of the premaxilla, and has only a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The postorbital process of the maxilla is massive, and has a broad horizontal articulation with the massive zygomatic process of the squamosal. The head of the squamosal bears a wide crest; the otic plate completely articulates with and broadly overlaps the ossified crista parotica. The dorsal part of the stapedial footplate is more than three times the length of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has an acuminate terminus between or slightly anterior to the level of the neopalatines. The sphenethmoid is ossified posterior to the midlength of the orbit, but is not synostosed with the prootic. The neopalatines are narrowly separated medially; each bears a low irregular ventral ridge. The pterygoid articulates with the squamosal via a ventromedial process of the zygomatic ramus of the latter; the pterygoid lacks a distinct dorsal ramus on its anterior ramus, and instead has a broad low dorsal expansion. The vomers bear moderately large dentigerous processes located at the level of the posterior margins of the choanae.

Life History

The eggs undergo direct development into froglets. One female (snout–vent length 78.8 mm) collected in September contained 14 eggs, about 7.0 mm in diameter each, in the brood pouch.

Advertisement Call

The call is an explosive “wrock,” usually followed one or two shorter notes, “rock-rock.”

Distribution and Ecology

Gastrotheca weinlandii occurs at elevations of 1100–2370 m on the Amazonian slopes of the Andes from southern Colombia to northern Peru (Fig. 10.39). In this region it inhabits cloud forest, where at night juveniles have been found on leaves of bushes and herbs, and adults at 2–10 m above the ground, on branches of trees.

Conservation Status

In the IUCN Red List, this species is listed as Data Deficient, with the statement that in Ecuador, the species is threatened by habitat destruction and degradation because of agricultural development for livestock and crops, in addition to forest clearance. It is less seriously threatened in Colombia and Peru. It does occur in

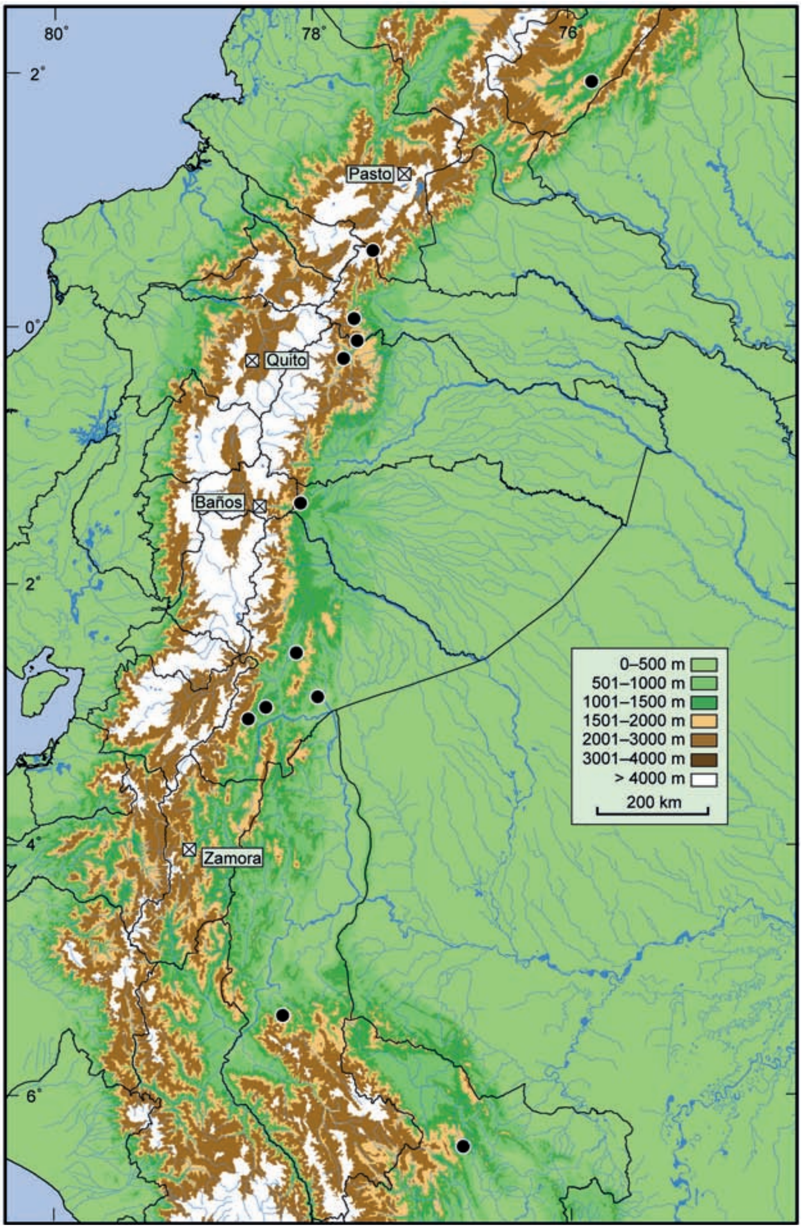

Fig. 10.39 Cordillera Oriental in Colombia, Ecuador, and Peru, showing the localities of known occurrences of *Gastrotheca weinlandii*.

some protected areas (e.g., Parque Nacional Natural Alto Fragua Indi Wasi in Colombia).

Etymology

Although not so stated on the original description, the specific name *weinlandii* is a patronym for the German zoologist David Friedrich Weinland, who was one of the authors of the description of *Notodelphys ovifera* (Lichtenstein and Weinland, 1854) and, in the same year, published a detailed study of embryonic stages of that species (Weinland, 1854).

Remarks

In juveniles having snout–vent lengths of 25 mm or less, the skin is not co-ossified with the underlying cranial elements. Also, juveniles tend to be paler than adults and have a dark brown postorbital bar continuous onto the flank until about midbody.

In discussing features of the holotypes of *Nototrema weinlandii* Steindachner, 1892, and *Hyla pusilla* Melin, 1941, Duellman (1974) concluded that the holotype of the latter was a juvenile of the former. He also erroneously placed *Gastrotheca bufona* Cochran and Goin, 1970, in the synonymy of *G. weinlandii*, a mistake that he corrected subsequently (Duellman, 1983).

Subgenus *Australotheca*, new subgenus

Australotheca Duellman. Type species—*Gastrotheca microdiscus* Andersson *in* Lönnberg and Andersson, 1910:9.

Definition

The species in the subgenus *Australotheca* are moderately large frogs; the mean ratio of tibia length to snout–vent length is less than 55%. These frogs have moderately large heads. The mean percentage of head length to snout–vent length is 36.2%–39.8%, and the relative percentage of head length to head width is 34.6%–37.0%. Members of this subgenus also have proportionally broad interorbital distances, because of the wide lateral flanges on the frontoparietals; the ratio of the interorbital distance to the head width is 37.0%–40.9%. The width of the upper eyelid is less than 65% of the interorbital distance; the ratio ranges from 48.4% in *Gastrotheca albolineata* to 61.2% in *G. ernestoi*. The hands are moderately large. The fingers are long, and bear large round terminal discs. Finger I is equal to or longer than Finger II.

The osteological data available for the species included in this subgenus strongly support their relationship. Each member has a sculptured sphenethmoid and a homogeneous pattern of dermal sculpturing across the skull table. The skull is characterized by wide supraorbital flanges and expansion of the posterolateral part of the frontoparietal over the epiotic eminences. The carotid canal is open, because the frontoparietal is not fused to underlying bones in the otic region. The squamosal bears a narrow crest; the zygomatic ramus is complete to the maxilla. The dentigerous processes of the vomers are located between the middle quadrants of the choanae. The neopalatines are smooth and unornamented ventrally.

Reproduction

Members of this subgenus produce eggs that undergo direct development into froglets (unconfirmed in *Gastrotheca fulvorufa*). Complete clutches are known for *G. albolineata* and *G. ernestoi*; in these two species clutch size varies from 16 to 24 eggs.

Distribution

Members of this subgenus inhabit the Atlantic Coastal Forest in southeastern Brazil, from southern Espírito Santo to Santa Catarina. The species principally occur at elevations of up to 1400 m in the mountain ranges in southeastern Brazil: Serra dos Órgãos, Serra do Mar, Serra da Bocaina, Serra de Mantiqueira, and inland to the Serra do Brigadeiro, in the state of Minas Gerais.

Content

Four species.

Etymology

The name is derived from the Latin *australis*, meaning "southern," and the Greek *theke*, meaning "container." The name refers to the southern distribution of the subgenus.

Remarks

Blackburn and Duellman's (2013) maximum likelihood analysis of four genes revealed that the southeastern Brazilian *Gastrotheca* were in a separate clade from the larger casque-headed species in northeastern Brazil; this difference was implied by data presented by Teixeira et al. (2012) and confirmed herein (chapter 3). As shown in Fig. 10.40, *G. albolineata* is the sister species to other members of the subgenus; it differs from all the others by its coloration and greater amount of webbing between the outer fingers.

Gastrotheca (*Australotheca*) *albolineata* (Lutz and Lutz)

Hyla albolineata Lutz and Lutz, 1939:69.—Holotype: AL-MN 1778 from Teresópolis, Estado do Rio de Janeiro, Brazil.

Gastrotheca albolineata—Sachsse, Izecksohn, and Carvalho-e-Silva, 1999:401.

Diagnosis

In this medium-sized species, adults of both sexes attain a snout–vent length of 60 mm. The tibia length is

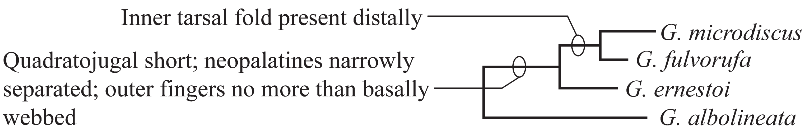
Inner tarsal fold present distally
Quadratojugal short; neopalatines narrowly separated; outer fingers no more than basally webbed
G. microdiscus
G. fulvorufa
G. ernestoi
G. albolineata

Fig. 10.40 Hypothesized phylogenetic relationships among species of the subgenus *Australotheca*, based on molecular data, with selected morphological synapomorphies noted.

KEY TO SPECIES OF SUBGENUS *AUSTRALOTHECA*

1. Outer fingers one-half webbed; dorsum green, with white labial, postorbital, heel, and supracloacal stripes .... *G. albolineata*
   Outer fingers no more than basally webbed; coloration not as described 2
2. Broad postorbital stripe fragmented; white supracloacal stripe; inner tarsal fold on distal half of tarsus; two to eight enlarged tubercles ventrolateral to cloacal opening .... *G. fulvorufa*
   Postorbital stripe not fragmented; no white supracloacal stripe; inner tarsal fold, if present, only on distal one-fourth of tarsus; no enlarged tubercles ventrolateral to cloacal opening 3
3. Outer toes about two-fifths webbed; inner tarsal fold present on distal one-fourth of tarsus....... *G. microdiscus*
   Outer toes webbed basally; inner tarsal fold absent .... *G. ernestoi*

less than 50% of the snout–vent length, and is longer than the foot. The interorbital distance is about twice the width of the eyelid. The skin on the dorsum is finely granular, not co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent; the heel lacks a calcar or tubercles. The tympanic annulus is smooth. The first finger is longer than the second. The discs are slightly wider than the adjacent digits. The outer fingers are more than one-half webbed; on the toes, the webbing extends to the penultimate subarticular tubercle on the fourth toe and the distal subarticular tubercle on the fifth toe. The dorsum is green, with two pairs of brown spots and narrow white lines. The head markings consist of a pale brown canthal stripe and a narrow dark brown labial stripe, bordered above by a pale yellow stripe. A pale dorsolateral stripe is present. The flanks are green, with a diagonal white stripe anteriorly; the venter is pale green.

Gastrotheca albolineata most closely resembles *G. microdiscus*, which differs by being larger (snout–vent length up to 75 mm) and by having a proportionately greater interorbital distance, no webbing between the outer fingers, a dark canthal stripe, no pale labial stripe, and tan flanks, with brown spots. *G. albolineata* also resembles *G. andaquiensis* and *G. longipes*, both of which are larger (snout–vent length to 76 and 83 mm, respectively) and have the first and second fingers equal in length, less webbing between the outer fingers, and a granular tympanic annulus. *G. andaquiensis* also differs by having an elongate calcar, prominent supraciliary process, brown flanks, and mottled brown dorsum, whereas in *G. longipes* the dorsum and flanks are green, with or without brown or white spots.

Description

The following description is based on 10 adults. The body is moderately robust; the maximum snout–vent length is 60 mm in males and females. The head is slightly wider than long, but not as wide as body. The snout is rounded in dorsal view, and is abruptly inclined from the nostrils to the tip in profile. The canthus rostralis is rounded. The loreal region is slightly concave; the lips are rounded. The top of the head is flat. The interorbital distance is slightly less than twice the width of the upper eyelid. The nostrils are slightly protuberant laterally at a point well behind the anterior margin of the lower jaw. The tympanum is round, and is separated from the eye by a distance about equal to the diameter of the tympanum. The tympanic annulus is smooth. The supratympanic fold is moderately weak, barely obscures the upper part of the tympanum, and extends from the posterior border of the orbit to a point above the insertion of the arm.

The arm is moderately robust; ulnar tubercles are absent. The hand is moderate in size. The fingers are long, and bear moderately large round discs; the width of the disc on the third finger is slightly less than the length of the tympanum. The relative lengths of the fingers are I > II < IV < III. The webbing is basal between the second and third fingers, and extends to the penultimate subarticular tubercle on the outer side of the third finger and the base of the disc on the fourth finger. Narrow lateral fringes are present on the fingers. The subarticular tubercles are large and round; none are bifid. Supernumerary tubercles are prominent on the proximal segments of the second, third, and fourth fingers. The palmar tubercle is low and round; the prepollical tubercle is elongately ovoid; nuptial excrescenses are absent. The hind limbs are moderately robust. The tibia length is slightly less than 50% of the snout–vent length; the foot length is about 43% of the snout–vent length. A calcar and tarsal tubercles are absent; an inner tarsal fold is absent. The inner metatarsal tubercle is ovoid, elevated, and visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. The toes are about three-fourths webbed; the webbing formula is **I**2—2**II**1½—2**III**1—2**IV**2—1**V**. The subarticular tubercles are large, round, and elevated; the supernumerary tubercles are large, round, and present only on the proximal segments of the toes.

The skin on the dorsal surfaces of the head, body, and limbs and on the flanks is finely granular; the skin on the belly and posteroventral surfaces of the thighs is coarsely granular. Cloacal tubercles are absent; the cloacal folds are weak and vertical. The opening of the brood pouch is broadly U-shaped, with the anterior margin posterior to the level of the sacrum. The dentigerous processes of the vomers are slightly posteromedially inclined to nearly transverse, and widely separated medially between the round choanae. Each process bears five to seven teeth. The tongue is nearly round, narrowly notched posteriorly, and free behind for about one-third of its length. The vocal slits extend posterolaterally from the base of the tongue.

COLOR IN PRESERVATIVE

The dorsum and venter are cream, with or without small dark brown spots. There is a conspicuous white dorsolateral stripe; a white supracloacal stripe is bordered below by brown. There is a brown stripe across the heel and along the outer edge of the tarsus, including on the dorsal surfaces of the fifth toe and the web between the fourth and fifth toes, but not on the disc on the fourth toe.

COLOR IN LIFE

The dorsum is bright green, with a few small reddish-brown spots (Fig. 10.41), usually a pair in the scapular region and another pair in the sacral region; some individuals have one or two small spots on the top of the head. The margin of the upper lip bears a white stripe that broadens as it extends onto the flanks, where it is bordered above by a narrow reddish-brown stripe. A white stripe on the heel extends diffusely along the outer edge of the foot, where it is bordered below by a reddish-brown stripe. Toes IV and V, and the webbing between them, are reddish brown, but the discs are pale green. There is a prominent white supracloacal stripe bordered below by reddish brown. Narrow pale green transverse lines are barely visible on the dorsal surfaces of the thighs and shanks. The ventral surfaces are pale green; the vocal sac in calling males is dark green. The iris is pale gold, with fine reddish-brown reticulations and flecks.

MEASUREMENTS

The sizes of the two adult females fall within the range of variation of the seven males available (Table 10.13).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, bear a homogeneous pattern of coarse pit-and-ridge dermal sculpturing. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange and a small otic flange. A temporal arcade is incomplete. The frontoparietal covers the anterior epiotic eminence, but is not fused with it; therefore the carotid canal is open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at an angle that exceeds 46°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for more than 75% of the the length of the rostrum. The pars facialis is

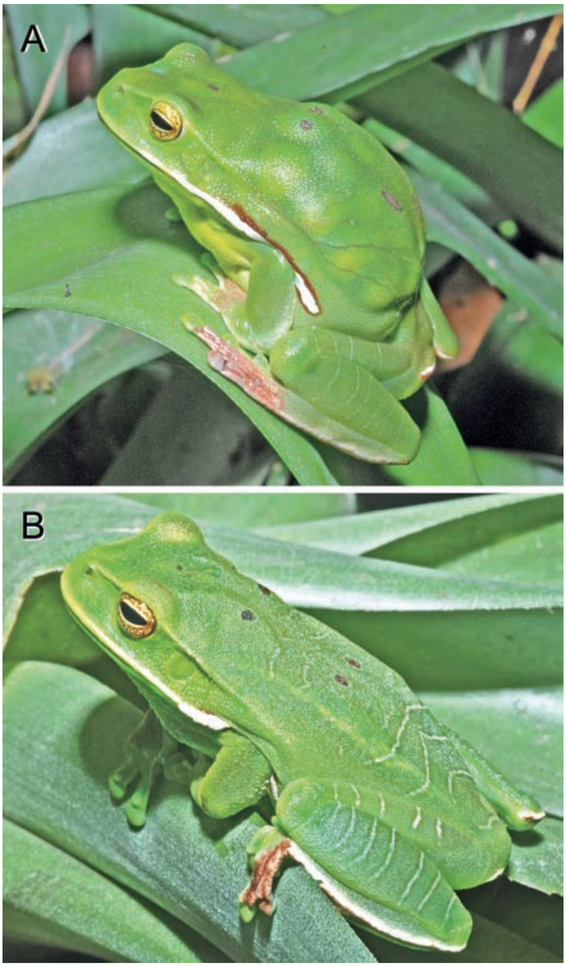

Fig. 10.41 *Gastrotheca albolineata.* A: MNRJ 54401, female, 60.1 mm SVL, Parque Estadual Três Picos, 900 m, Rio de Janeiro, Brazil. B: MNRJ 75915, male, 55.0 mm SVL, Saquarema, Rio de Janeiro, Brazil. Photos by J. P. Pombal Jr., KUDA.

Table 10.13 Univariate statistics for adults of *Gastrotheca albolineata*

	Males ($n = 7$)			Females ($n = 2$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	45.7	30.6–59.3	9.94	59.5	50.0–59.9	0.64
Tibia length	23.6	18.1–27.0	3.22	28.4	28.0–28.8	0.57
Foot length	21.1	13.7–25.7	4.12	25.6	25.1–26.0	0.64
Head length	17.7	14.3–21.5	2.39	21.0	20.4–21.5	0.78
Head width	19.0	14.3–23.9	3.18	22.7	22.5–22.9	0.28
Interorbital distance	7.8	5.0–9.5	1.70	9.3	8.1–10.4	1.63
Eyelid width	3.9	3.0–4.6	0.71	4.9	4.5–5.2	0.49
Internarial distance	4.2	3.1–5.1	0.75	5.0	4.8–5.1	0.21
Eye diameter	4.9	4.4–5.3	0.31	5.5	5.2–5.8	0.42
Eye–nostril distance	4.9	4.0–6.8	1.01	5.5	5.3–5.8	0.85
Orbit–jaw distance	2.4	2.1–3.0	0.33	2.8	2.5–3.0	0.35
Nostril–jaw distance	3.7	3.1–4.1	0.42	4.1	3.8–4.4	0.42
Tympanum diameter	3.4	3.0–4.1	0.42	4.0	3.8–4.1	0.21
Thumb length*	10.3	9.9–11.0	0.43	12.0	11.8–12.1	0.21
Third finger length	16.1	13.9–18.5	2.01	19.0	18.5–19.5	0.71
Disc width	2.6	1.8–3.3	0.59	3.6	3.4–3.7	0.21

*Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

distinctly separated from the alary process of the premaxilla, and has only a narrow overlap with the dental process of the premaxilla. The quadratojugal is of moderate length. The postorbital process of the maxilla is low but distinct, and has a narrow articulation with the slender zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the otic ramus completely articulates with and broadly overlaps the ossified crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in length, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified posterior to the midlength of the orbit, but is not synostosed with the prootic. The neopalatines are widely separated medially, and are unornamented ventrally. The pterygoid articulates with the medial side of the zygomatic ramus of the squamosal via an acuminate recurved dorsal ramus on the anterior ramus of the pterygoid. The vomers bear moderately large dentigerous processes located between the middle quadrants of the choanae.

Life History

Eggs hatch as froglets. A female obtained on 21 September 2008 had a snout–vent length of 59.0 mm and contained 22 eggs, with a maximum diameter of 7.4 mm, in the pouch. A female with a snout–vent length of 59.9 mm gave birth on 8 December 1995 to 16 froglets having snout–vent lengths of 16.3–17.3 mm ($\bar{x} = 16.84 \pm 0.352$). Males call as early as July. A juvenile having a snout–vent length of 23.8 mm was found in January.

Advertisement Call

Izecksohn and Carvalho-e-Silva (2008) summarized data from eight recordings from the Parque Nacional Serra dos Orgãos. The call consists of 5–14 short notes (mean duration = 70 milliseconds) with a dominant frequency of 1.2–1.7 kHz and fundamental frequency of 0.500–0.800 kHz.

Distribution and Ecology

Gastrotheca albolineata is an inhabitant of the Atlantic Coastal Forest at elevations of 90–1400 m in the Serra do Mar from southern Espírito Santo to coastal São Paulo in southeastern Brazil (Fig. 10.42). Most individuals have been found on the leaves and branches of bushes and trees at night, but one was on the forest floor (Gressler et al., 2008; Pontes et al., 2012). In addition to the specimens examined, Pontes et al. (2012) reported this species from the Parque Nacional da Serra da Bocaina and from Sampaio Corréa in Estado do Rio de Janeiro; males were calling at theses sites on 1 and 10 August 2011.

Conservation Status

In the IUCN Red List this species is categorized as being of Least Concern, because of its apparent abundance and existence in several protected areas. Pontes

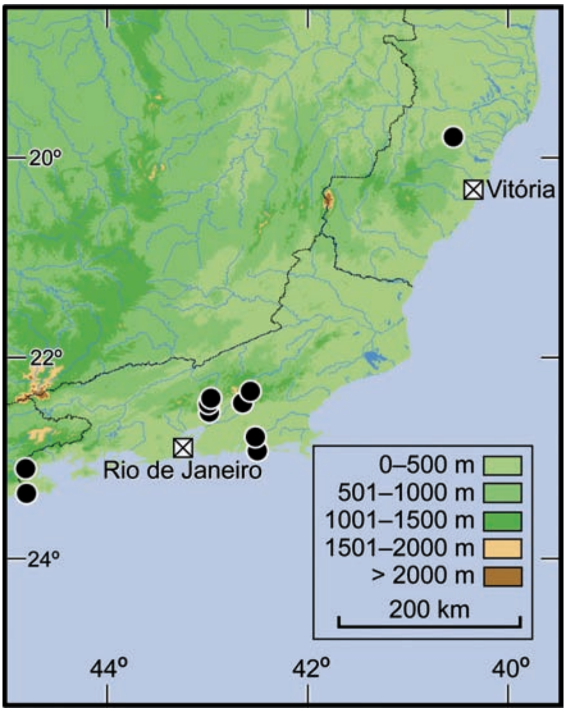

Fig. 10.42 Southeastern Brazil, showing the localities of known occurrences of *Gastrotheca albolineata*.

et al. (2012) suggested that the species should be categorized as Data Deficient.

Etymology

The specific name is an adjective derived from the Latin *albus*, meaning "white," and the Latin *lineatus*, meaning "line," referring to the white lines on the flanks.

Remarks

The holotype (AL-MN 1778) is a small male with a 30.8 mm snout–vent length, and it has faded to a nearly uniform creamy tan. A. Lutz and B. Lutz (1939) only examined a male and therefore considered the frog to be a species of *Hyla*. Bertha Lutz reported a second specimen (MNRJ 3223), also a male, and commented (Lutz, 1973:235): "*Hyla albolineata* does not show any affinity with the other green species of *Hyla*. It is even possible that it may be a *Gastrotheca*." Sachsse et al. (1999) confirmed the generic placement.

A subadult male (MBML 47), having a snout–vent length of 30.6 mm, from Distrito Santa Teresa, Espírito Santo, about 400 kilometers northeast of the localities in Rio de Janeiro, differs by having a granular supratympanic fold that curves downward behind the tympanum. In other structural features and coloration, this specimen is like those from Rio de Janeiro.

Gastrotheca (*Australotheca*) *ernestoi* Miranda-Ribeiro

Gastrotheca ernestoi Miranda-Ribeiro, 1920:323.—Holotype: MZUSP 238 from "Serra do Macahé" [= Municipality of Macaé, fide Caramaschi and Rodrigues, 2007:3], Estado do Rio de Janeiro, Brazil.

Gastrotheca viridis Lutz and Lutz, 1939:81.—Holotype: AL-MN 969 from Bonito, Serra da Bocaina [= Fazenda do Bonito, Municipality of São José do Berreiro, fide Caramaschi and Rodrigues, 2007:4], Estado do São Paulo, Brazil. Synonymy fide Caramaschi and Rodrigues, 2007:4.

Gastrotheca longipes (in part)—Goin, 1964:347.

Gastrotheca microdisca (in part)—Duellman, 1984:305.

Gastrotheca (*Opisthodelphys*) *viridis*—Dubois, 1987:31.

Gastrotheca (*Opisthodelphys*) *ernestoi*—Dubois, 1987:31.

Diagnosis

This moderately large species attains a maximum snout–vent length of 70 mm. The tibia length is less than 55% of the snout–vent length, and is slightly longer than the foot. The interorbital distance is about twice the width of the upper eyelid. The skin on the dorsum is smooth, not co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercles. The tympanic annulus is smooth. The first finger is longer than the second; the disks are much wider than the digits proximal to the discs. The outer fingers are webbed basally; on the foot the webbing extends maximally to a point just distal to the antepenultimate subarticular tubercle on the fourth toe and the distal subarticular tubercle on the fifth toe. The dorsum is tan or brown, with darker brown irregular markings. Markings on the head consist of a dark brown canthal stripe and postorbital stripes, and a suborbital spot. A pale dorsolateral stripe is absent. The flanks are tan to brown, with diagonal brown marks. The venter is white.

Among the species of *Gastrotheca* in eastern and southeastern Brazil, *G. ernestoi* is most like *G. fulvorufa* and *G. microdiscus*, both of which have an inner tarsal fold at least distally on the tarsus. Moreover, *G. fulvorufa* differs by having two to eight tubercles below the cloacal opening (none in *G. ernestoi*), and *G. microdiscus* differs by lacking basal webbing between the outer toes. The much larger *G. fissipes*, *megacephala*, *prasina*, and *recava* differ from *G. ernestoi* by having casqued co-ossified heads and Finger I much longer than Finger II. The same relative finger lengths also are present in *G. albolineata*, *flamma*, and *pulchra*. The former differs from *G. ernestoi* by being green, with a prominent white postorbital stripe, whereas *G. flamma* and

G. pulchra differ from *G. ernestoi* by having calcars on the heels and one or two tubercles on the outer edges of the upper eyelids, features not present in *G. ernestoi*.

Description

The following description is based on nine adults. The body is moderately robust; the maximum snout–vent length is 68.0 mm in males, and 69.6 mm in females. The head is slightly wider than long, but not as wide as the body. The snout is rounded in dorsal view, and is round to bluntly rounded in profile. The canthus rostralis is rounded. The loreal region is shallowly concave; the lips are rounded. The top of the head is flat. The interorbital distance is about twice the width of the upper eyelid. The nostrils are not protuberant, and are directed laterally at a point behind the level of the anterior margin of the lower jaw. The tympanum is round, and is separated from the eye by a distance about 1.5 times the diameter of the tympanum. The tympanic annulus is smooth. The supratympanic fold is moderately weak, barely obscures the upper part of the tympanum, and curves posteroventrally to a point above the insertion of the arm.

The arm is moderately robust; ulnar tubercles are absent. The hand is moderately large. The fingers are long, and bear moderately large round discs; the width of the disc on the third finger is slightly less than the length of the tympanum. The relative lengths of the fingers are I ≥ II < IV < III. Webbing is absent between the inner fingers, and is basal between Fingers III and IV. The subarticular tubercles are low and round; none are bifid. Supernumerary tubercles are small, subconical, and present only on Finger III. The palmar tubercle is low, and diffuse or weakly bifid; the prepollical tubercle is elliptical; nuptial excrescences are not evident. The hind limbs are rather slender. The tibia length is about 50% of the snout–vent length; the foot length is about 45% of the snout–vent length. A calcar and tarsal tubercles are absent; an inner tarsal fold and outer metatarsal tubercle also are absent. The inner metatarsal tubercle is ovoid, elevated, and barely visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. The toes are about three-fourths webbed; the webbing formula is **I**1—1**II**1^{+}—2^{-}**III**1—2**IV**2—1**V**. The subarticular tubercles are small and round; supernumerary tubercles are absent.

The skin on the dorsum is smooth in females, and smooth or finely granular in males; in large adults the skin is not co-ossified with the skull. The skin on the belly and posteroventral surfaces of the thighs is coarsely granular. Cloacal tubercles and folds are absent. The opening of the brood pouch is broadly U-shaped, with the anterior margin at the posterior edge of the sacrum. The dentigerous processes of the vomers are slightly inclined posteriorly, and are narrowly separated medially between small round choanae. Each process bears four to six teeth. The long slit-like vocal slits extend posterolaterally from the base of the tongue.

COLOR IN PRESERVATIVE

The dorsum is tan, with irregularly shaped and variously sized brown spots. The flanks are tan; some individuals have brown spots or two diagonal bars posteriorly. The venter is cream. A pale dorsolateral stripe is absent. Markings on the head consist of a dark spot or circle on the upper eyelid, a dark brown to black canthal stripe, a suborbital brown bar on the upper lip, and a narrow to broad postorbital stripe, usually encompassing the tympanum that curves posteroventrally to the midflank. Dark brown transverse limb bars usually consist of one or two on the forearm and two or three each on the thigh, shank, and tarsus. A dark brown cloacal patch usually lacks a pale stripe above.

COLOR IN LIFE

Color photographs of an adult male (Izecksohn and Carvalho-e-Silva, 2008) reveal a brown dorsum, with darker brown markings, a faint creamy white labial stripe, and dark blue posterior surfaces of the thighs. The iris appears to be reddish brown (Fig. 10.43).

MEASUREMENTS

Females are only slightly larger than males (Table 10.14); no significant differences exist between the sexes

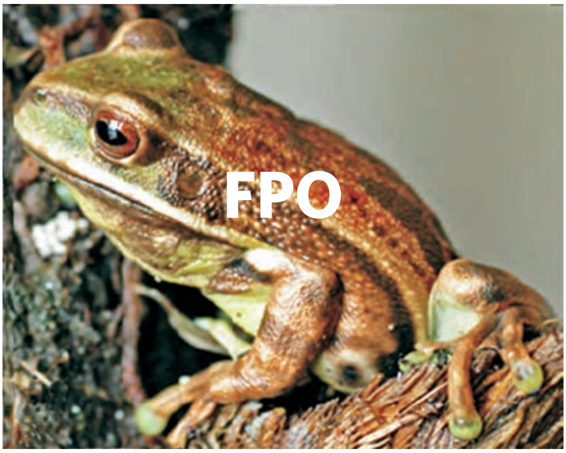

Fig. 10.43 *Gastrotheca ernestoi* (ZUFRJ 2534), male, Parque Nacional da Serra dos Órgãos, Rio de Janeiro. Brazil. Photo by S. Carvalho-e-Silva, KUDA.

Table 10.14 Univariate statistics for adults of *Gastrotheca ernestoi* and *G. fulvorufa*

		G. ernestoi (4 males, 4 females)			*G. fulvorufa* (5 males, 3 females)		
Character	Sex	Mean	Range	SD	Mean	Range	SD
Snout–vent length	males	60.4	52.7–68.0	6.46	64.2	61.3–68.8	2.77
	females	63.0	57.8–69.6	5.09	69.4	65.2–76.5	6.18
Tibia length	males	29.2	25.3–31.3	2.76**	34.5	32.5–37.0	1.62
	females	31.9	29.6–33.2	1.59†	38.5	34.8–42.6	3.91
Foot length	males	26.7	22.0–30.5	3.75	30.0	28.3–32.8	1.82
	females	28.8	27.0–30.3	1.56	30.9	29.2–33.5	2.31
Head length	males	20.9	18.3–22.3	1.87	22.2	20.5–24.0	1.48
	females	22.9	20.7–24.5	1.60	24.0	23.0–25.4	1.27
Head width	males	21.2	18.5–23.5	2.13	23.0	21.5–25.4	1.57
	females	24.0	22.2–26.3	1.73	25.4	24.2–26.7	1.25
Interorbital distance	males	8.0	6.7–9.1	1.14	9.2	7.7–10.4	1.09
	females	9.1	7.7–10.0	1.03	10.1	9.2–10.7	0.78
Eyelid width	males	5.1	4.8–5.4	0.25	5.4	4.7–5.9	0.44
	females	5.3	4.5–6.2	0.88	5.1	4.6–5.8	0.61
Internarial distance	males	4.5	3.5–5.2	0.74	5.3	4.7–5.6	0.36
	females	5.4	4.5–6.3	0.81	5.1	4.6–5.4	0.46
Eye diameter	males	6.1	5.8–6.4	0.26	6.6	6.1–7.5	0.52
	females	6.7	5.9–7.3	0.63	6.2	5.4–7.1	0.85
Eye–nostril distance	males	5.7	5.2–6.2	0.48	6.7	6.0–8.2	0.84
	females	6.1	5.3–6.8	0.63	6.9	6.8–7.0	0.10
Orbit–jaw distance	males	3.3	2.8–3.6	0.36	3.4	2.8–3.8	0.38
	females	3.4	3.0–3.8	0.37	3.6	3.5–3.7	0.14
Nostril–jaw distance	males	4.8	3.8–5.4	0.71	4.9	4.2–5.3	0.42
	females	5.1	4.6–5.5	0.39	4.8	4.7–4.8	0.07
Tympanum diameter	males	3.8	3.3–4.1	0.36	4.0	3.7–4.6	0.35
	females	4.4	3.6–4.9	0.60	3.9	3.1–4.6	0.76
Thumb length	males	12.1	11.0–13.5	1.27	13.1	12.4–13.9	0.59
	females	13.5	12.7–14.0	0.58	13.8	12.1–15.5	2.40
Third finger length	males	19.1	15.8–22.5	3.35	20.6*	20.0–21.2	0.51
	females	20.6	19.5–21.5	0.83	23.2*	21.6–24.8	2.26
Disc width	males	3.0	2.4–3.7	0.56	3.6	2.6–4.5	0.80
	females	3.4	2.7–4.0	0.56	3.3	2.5–4.0	1.06

*Differences between the means of the sexes are significant (ANOVA, $P \leq 0.05$).

†Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

**Differences between the means of the two species are significant (ANOVA, $P \leq 0.01$).

in the small sample available. One individual was partially destroyed, thereby making some measurements impossible, so it is not included in the table.

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, bear a homogeneous pattern of semicoarse pit-and-ridge dermal sculpturing. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange and a small otic flange. A temporal arcade is incomplete. The frontoparietal covers the anterior epiotic eminence, but is not fused with it; therefore the carotid canal is open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for more than 75% of the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has only a narrow overlap with the dental process of the premaxilla. The quadratojugal is short. The postorbital process of the maxilla is low but distinct, and has a moderately wide articulation with the broad zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the otic ramus completely articulates with and broadly overlaps the ossified crista parotica. The dorsal part of the stapedial footplate is more than three times the length of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are widely separated medially, and are unornamented ventrally. The pterygoid articulates with the medial side of the zygomatic ramus of the squamosal via a broad triangular dorsal flange on the anterior ramus of the pterygoid; the flange articulates with the medial surfaces of both the zygomatic ramus of the squamosal and the postorbital process of the maxilla. The vomers bear moderately large dentigerous processes located between the middle quadrants of the choanae.

Life History

The female holotype (snout–vent length 60.5 mm) contained 24 eggs, each 8 mm in diameter, in the pouch (Miranda-Ribeiro, 1920). Another female (MNRJ 19329), having a snout–vent length of 64.0 mm, contained 20 young about to hatch in the pouch. The gill stalks from the two branchial arches on each side were fused, as were the gills on each side of the head.

Advertisement Call

Izecksohn and Carvalho-e-Silva (2008) provided data on recordings of two individuals. The call consists of two notes, each approximately 400 milliseconds in duration. The first note consists of seven pulses, and the second note, three pulses. The dominant frequency is about 1.12 kHz. These authors noted the similarity of the call of *Gastrotheca ernestoi* with that of the Bare-throated Bellbird (*Procnias nudicollis*), in a possible case of mimicry (see the account of *G. microdiscus*).

Distribution and Ecology

Gastrotheca ernestoi occurs on the seaward slopes (up to 1000 m) of the Serra do Mar and the Serra da Mantiqueira in the states of Rio de Janeiro and extreme western São Paulo, and inland to the Serra do Brigadeiro, Minas Gerais, in southeastern Brazil (Fig. 10.44). The species inhabits dense rainforest and apparently lives mostly in the canopy.

Conservation Status

In the IUCN Red List, *Gastrotheca ernestoi* is categorized as Data Deficient. It does occur in some protected areas (e.g., Parque Nacional Serra dos Órgãos).

Etymology

The specific name *ernestoi* is a patronym for Ernesto Garbe, who collected the holotype.

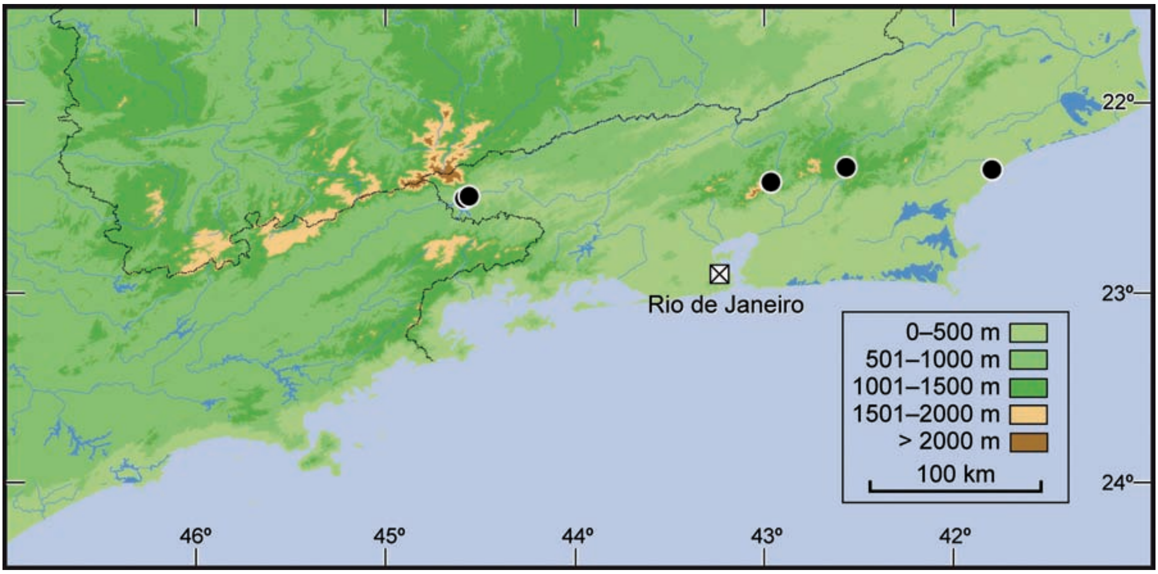

Fig. 10.44 Southeastern Brazil, showing the localities of known occurrences of *Gastrotheca ernestoi*.

Remarks

The placement of the nominal species, *Gastrotheca viridis* Lutz and Lutz, 1939, has been confused for half a century. Cochran's (1955:52) recognition of *G. viridis* was based solely on her reproducing the original description. Goin's (1964) placement of *G. viridis* in the synonymy of *G. longipes* Boulenger, 1882, was challenged by Duellman (1974:3), who stated: "Goin overlooked the coloration of the feet, which in *G. viridis* lack the dark outer edges and toes characteristic of *G. longipes*. Furthermore, *G. viridis* is known only from the Serra do Mar in southeastern Brasil, whereas *G. longipes* occurs in the upper Amazon Basin of Ecuador and Perú." In his review of Brazilian *Gastrotheca*, based on an examination of the few preserved specimens, Duellman (1984) placed *G. viridis* (as well as *G. ernestoi*) in the synonymy of *G. microdiscus*. Caramaschi and Rodrigues (2007) resurrected *G. ernestoi* from the synonymy of *G. microdiscus* and placed *G. viridis* in the synonymy of *G. ernestoi*; Izecksohn and Carvalho-e-Silva (2008) concurred with this placement. Having examined the holotypes of all of the nominal taxa, I also follow the arrangement of Caramaschi and Rodrigues (2007).

The holotype of *Gastrotheca ernestoi* (MZUSP 238; Fig. 10.45A) is a brooding female, 60.5 mm in snout–vent length, in good condition; the pouch, throat, and belly have been dissected. There is a dark brown circle, with small dark brown spots, on each eyelid. Similar small posteromedially diagonal marks are present in the occipital region; an elongate mark is present medially, anterior to the sacrum. A shorter mark is present dorsolaterally, on the left side; there is a pair of small marks lateral to the sacrum, and a pair of short dashes anterior to the opening of the pouch. Two narrow transverse marks are present on the dorsal surface of each thigh: three on the shank, and three on each foot. There is a dark brown cloacal patch. The outer toes are not dark brown. Narrow dark brown canthal and postorbital stripes are present; the latter extends to midflank, but there is no interorbital bar. The margin of the upper lip is dark brown. Finger I is longer than Finger II (contra Caramaschi and Rodrigues, 2007:7).

The holotype of *Gastrotheca viridis* (AL-MN 969; Fig. 10.45B) is a female, 57.8 mm in snout–vent length; the specimen is soft and faded. There is a brown semicircle on the median border of each eyelid, and several small brown spots or circles on the tan dorsum. The dorsum and the flanks lack diagonal or longitudinal marks. A dark brown canthal stripe and narrow postorbital stripe are present; the later is curved and terminates on the midflank. There is no interorbital bar. The margin of the upper lip is dark brown. The faded condition precludes any notation of bars on the limbs and a cloacal patch.

The dorsal coloration of each of these holotypes resembles that of some individuals of *Gastrotheca microdiscus* (Fig. 10.45C). The dark-bordered spots on the upper eyelids seem to be characteristic of all specimens of *G. ernestoi* and some specimens of *G. microdiscus*.

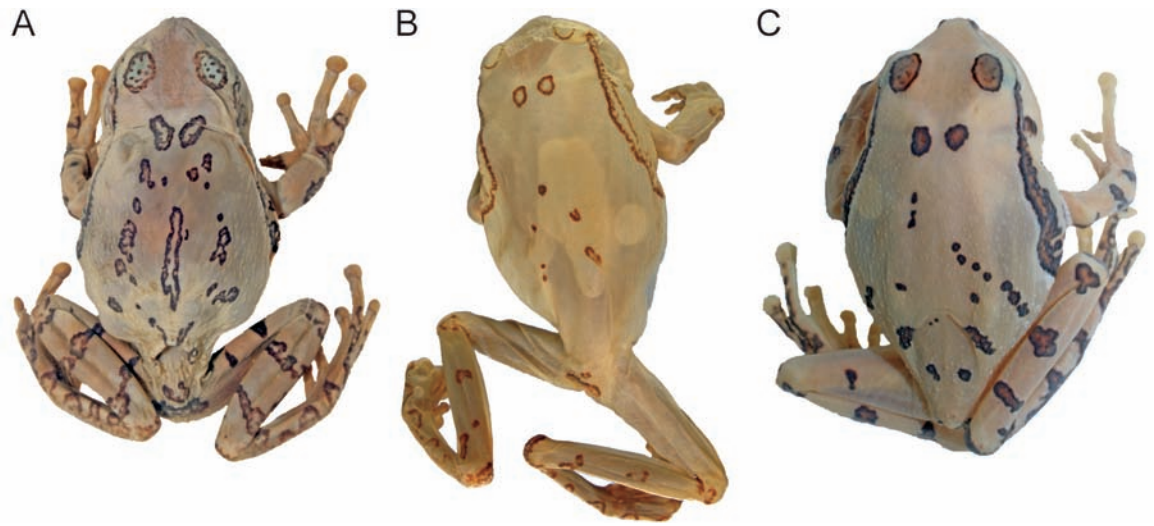

Fig. 10.45 Adult female *Gastrotheca*. A: *G. ernestoi* (MZUSP 238, holotype), 60.5 mm SVL. B: *G. viridis* (AL-MN 969, holotype), 57.8 mm SVL. C: *G. microdiscus* (MZUSP 101522), 58.8 mm SVL. Photos by M. Forlani (A and C) and I. Nunes (B), KUDA.

Gastrotheca (Australotheca) fulvorufa (Andersson)

Nototrema fulvorufa Andersson, 1911:3.—Holotype: NHRM 913 from near Santos [= Região de Paranapiacaba, Serra do Mar, fide Bokermann, 1966:77], Estado do São Paulo, Brazil.

Gastrotheca fulvorufa—Miranda-Ribeiro, 1926:110; Caramaschi and Rodrigues, 2007:6.

Hyla Parkeri DeWitte, 1930a:226.—Holotype: IRSNB 1026 from Réserve d'Alto da Serra, Estado do São Paulo, Brazil. Preoccupied by *Hyla parkeri* Gaige, 1929:1.

Hyla parkeriana DeWitte, 1930b:102. Replacement name for *Hyla Parkeri* DeWitte, 1930, preoccupied by *Hyla parkeri* Gaige, 1929.

Gastrotheca microdisca (in part).—Cochran, 1955:50; Duellman, 1984:305.

Diagnosis

This large species attains a maximum snout–vent length of 76.5 mm. The tibia length is about 55% of the snout–vent length, and is notably longer than the foot. The interorbital distance is about twice the width of the upper eyelid. The skin on the dorsum is finely granular, co-ossified or not with the dermal roofing bones of the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercles. The tympanic annulus is smooth. The first finger is slightly longer than the second; the disks are much wider than the digits proximal to the discs. The outer fingers are webbed basally; on the foot the webbing extends maximally to a point just distal to the antepenultimate subarticular tubercle on the fourth toe and the distal subarticular tubercle on the fifth toe. The dorsum is tan or brown, with darker brown irregular markings. Markings on the head consist of dark brown canthal and postorbital stripes and one or two suborbital spots. A pale dorsolateral stripe is absent. The flanks are tan to brown, with two or three diagonal brown marks. The venter is cream, with or without brown flecks.

Among the species of *Gastrotheca* in eastern and southeastern Brazil, *G. fulvorufa* is most like *G. ernestoi* and *G. microdiscus*, both of which lack enlarged tubercles below the cloacal opening; moreover, *G. microdiscus* lacks basal webbing between the outer fingers, and *G. ernestoi* differs by lacking a tarsal fold. The much larger *G. fissipes*, *megacephala*, *prasina*, and *recava* differ from *G. fulvorufa* by having casqued co-ossified heads, and Finger I much longer than Finger II. The same relative finger lengths also are present in *G. albolineata*, *flamma*, and *pulchra*; the former differs from *G. fulvorufa* by being green, with a prominent white postorbital stripe. *G. flamma* and *G. pulchra* differ from *G. fulvorufa* by having calcars on the heels and one or two tubercles on the outer edges of the upper eyelids, features not present in *G. fulvorufa*.

Description

The following description is based on seven adults. The body is moderately robust; the maximum snout–vent length is 68.8 mm in males, and 76.5 mm in females. The head is slightly wider than long, but not as wide as body. The snout is rounded in dorsal view, and is rounded to slightly inclined anteroventrally in profile. The canthus rostralis is rounded. The loreal region is shallowly concave; the lips are rounded. The top of the head is flat. The interorbital distance is about twice the width of the upper eyelid. The nostrils are not protuberant, and are directed laterally at a point behind the level of the anterior margin of the lower jaw. The tympanum is round, and is separated from the eye by a distance about 1.5 times the diameter of the tympanum. The tympanic annulus is smooth. The supratympanic fold is moderately weak, barely obscures the upper part of the tympanum, and curves posteroventrally to a point above the insertion of the arm.

The arm is moderately robust; ulnar tubercles are absent. The hand is moderately large. The fingers are long, and bear moderately large round discs; the width of the disc on the third finger is slightly less than the length of the tympanum. The relative lengths of the fingers are I ≥ II < IV < III. Webbing is absent between the inner fingers, and is basal between Fingers III and IV or Fingers II, III, and IV. The subarticular tubercles are small and round; none are bifid. The supernumerary tubercles are small, subconical, and present only on the proximal segments of Fingers III and IV. The palmar tubercle is low and round; the prepollical tubercle is elongately elliptical; nuptial excrescences are not evident. The hind limbs are rather slender. The tibia length is slightly more than 50% of the snout–vent length; the foot length is about 45% of the snout–vent length. A calcar and tarsal tubercles are absent; a thin inner tarsal fold is present on the distal half of the tarsus. An outer metatarsal tubercle is absent. The inner metatarsal tubercle is elongately ovoid, and is visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. The toes are about two-thirds webbed; the webbing formula is **I**1^{-}—2**II**1—2**III**1½—2^{-}**IV**(1½–2^{-})—1**V**. A dermal fringe extends from the distal edge of the inner metatarsal tubercle to the level of the distal subarticular tubercle on Toe I in some individuals. The subarticular tubercles are small and round; supernumerary tubercles are small and diffuse (absent or not on Toe I).

The skin on the dorsum is finely granular; in large adults the skin is partially co-ossified with the anterior parts of the frontoparietals. The skin on the belly and posteroventral surfaces of the thighs is coarsely granular. Cloacal folds are absent. Two to eight enlarged tubercles are present ventrolateral to the cloacal opening; the proximal ones are by far the largest. The opening of the brood pouch is broadly U-shaped, with the anterior margin at the posterior edge of the sacrum. The dentigerous processes of the vomers are nearly transverse, and are narrowly separated medially between small round choanae. Each process bears four to six teeth. The long slit-like vocal slits extend posterolaterally from the base of the tongue.

COLOR IN PRESERVATIVE

The dorsum is tan, with small brown flecks. The flanks are tan, with two or three dark brown diagonal marks; the throat and belly are cream, with or without brown flecks. A dark interorbital bar, a dark spot on each eyelid, and a pale dorsolateral stripe are absent. Markings on the head consist of a dark brown canthal stripe, and one or two narrow suborbital bars. A broad fragmented postorbital stripe passes across the tympanum and curves ventrally on the anterior half of the flank. There are narrow brown transverse bars on the dorsal surfaces of the limbs: two on each forearm, three on the thigh, three on the shank, and two or three on the foot. In some specimens a dark brown cloacal patch is bordered above by a white stripe.

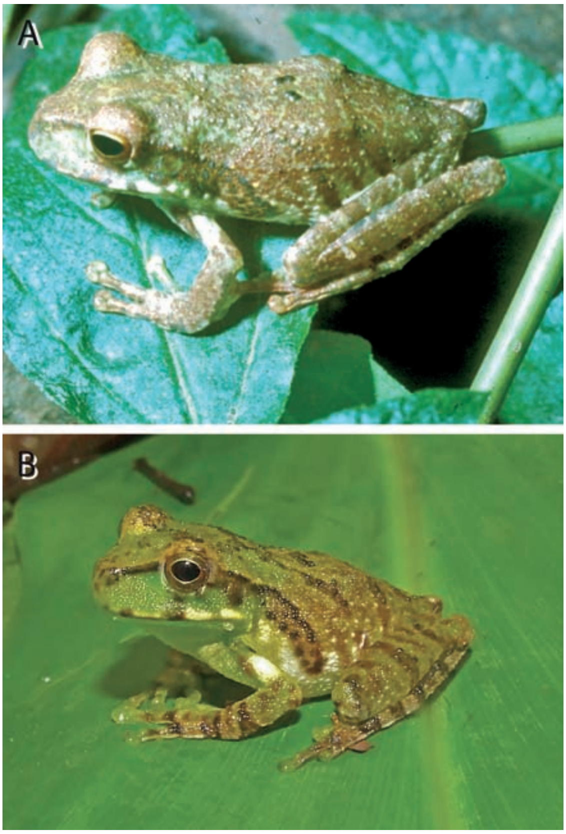

Fig. 10.46 *Gastrotheca fulvorufa*. A: adult male, Teresópolis, Rio de Janeiro, Brazil. B: MZUSP 143700, juvenile, Parque Natural Municipal Nascentes de Paranapiacaba, São Paulo, Brazil. Photos by E. Izecksohn, KUDA (A), and with permission granted by the photographer, Vivian Trevine (B).

COLOR IN LIFE

In Izecksohn and Carvalho-e-Silva (2008), color photographs of two adults reveal a reddish-brown dorsum with darker brown flecks, irregular black markings on the flanks, and a reddish-brown iris. A photograph of an adult male shows a mottled reddish-brown and pale green dorsum, and a reddish-brown iris (Fig. 10.46A). A photograph of a juvenile (MZUSP 143700) shows a greenish-tan dorsum with brown markings, a green throat and belly, and a brown iris (Fig. 10.46B).

MEASUREMENTS

Males are slightly larger than females (Table 10.14).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, bear a homogeneous pattern of coarse pit-and-ridge dermal sculpturing. The nasals articulate medially, but are independent of one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange, and has a moderate-sized otic flange. The temporal arcade is incomplete. The frontoparietal covers the anterior epiotic eminence, but is not fused with it; therefore the carotid canal is open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for more than 75% of the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has only a narrow overlap with the dental process of the premaxilla. The quadratojugal is short. The postorbital process of the maxilla is indistinct or absent, and has a narrow articulation with the slender zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the otic ramus completely articulates with and moderately overlaps the ossified crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in length, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are moderately separated medially, and are unornamented ventrally. The pterygoid articulates with the medial side of the zygomatic ramus of the squamosal via a broad low dorsal flange on the anterior ramus of the pterygoid; the flange articulates with the medial surface of the postorbital process of the maxilla. The vomers bear moderately large dentigerous processes located between the middle quadrants of the choanae.

Life History

No brooding *Gastrotheca fulvorufa* females have been found. Nonetheless, females of this species are most likely to produce large eggs that undergo direct development, like the other members of the genus is eastern and southeastern Brazil.

Advertisement Call

Izecksohn and Carvalho-e-Silva (2008) described the call as consisting of two notes, the first much longer than the second (16 and 6 milliseconds), and both lacking distinct pulses. The dominant frequency of both notes is about 1.785 kHz.

Distribution and Ecology

Gastrotheca fulvorufa inhabits humid forest on the slopes of the Serra do Mar in the states of Rio de Janeiro and São Paulo in southeastern Brazil (Fig. 10.47). This is an arboreal species that apparently is mostly confined to the canopy.

Conservation Status

According to the IUCN Red List, the conservation status is Data Deficient. This species does occur in the Parque Nacional da Serra das Orgãos, where it is protected.

Etymology

The specific name is derived from the Latin adjective *fulvus*, meaning "tawny," and the Latin noun *rufus*, meaning "red"; the name was applied by Andersson (1911) in reference to the dorsal coloration of the type specimen.

Remarks

Cochran (1955) synonymized *Hyla Parkeri* De Witte, 1930 (non *Hyla parkeri* Gaige, 1929), with *Gastrotheca microdiscus* (Andersson, 1910). Both Cochran (1955) and Duellman (1984) placed *Nototrema fulvorufa* Andersson, 1911, in the synonymy of *G. microdiscus*. Caramaschi

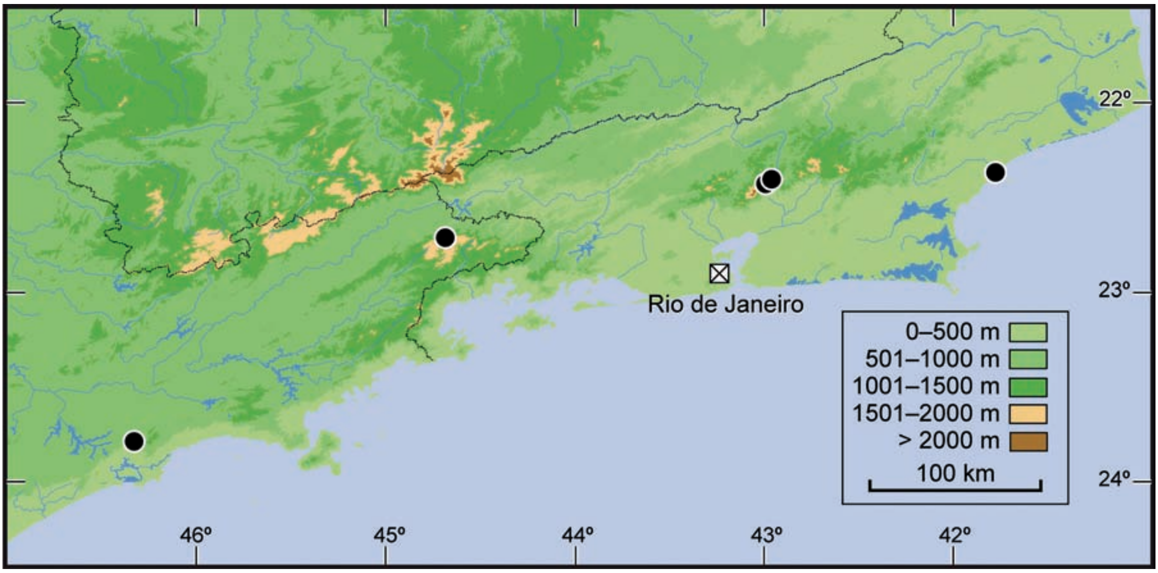

Fig. 10.47 Southeastern Brazil, showing the localities of known occurrences of *Gastrotheca fulvorufa*.

and Rodrigues (2007) recognized *G. fulvorufa* as a distinct species; this arrangement was supported by data provided by Izecksohn and Carvalho-e-Silva (2008). Consequently, *Hyla Parkeri* De Witte is placed in the synonymy of *Gastrotheca fulvorufa*.

Gastrotheca (*Australotheca*) *microdiscus* (Andersson)

Nototrema microdiscus Andersson *in* Lönnberg and Andersson, 1910:9.—Syntypes: NHRM 1480 [2 specimens] from "Desiro Ribas" [= Desvio Ribas], Estado do Paraná, Brazil.

Opisthodelphis microdiscum—Miranda-Ribeiro, 1926:112.

Gastrotheca microdisca—Cochran, 1955:50; Duellman, 1984: 305.

Gastrotheca (*Opisthodelphis*) *microdiscus*—Dubois, 1987:31.

Gastrotheca microdiscus—Caramaschi and Rodrigues, 2007:5.

Diagnosis

This moderately large species attains a maximum snout–vent length of 54.0 mm. The tibia length is more than 50% of the snout–vent length, and is notably longer than the foot. The interorbital distance is slightly less than twice the width of the upper eyelid. The skin on the dorsum is smooth in females, and has scattered small tubercles in males; it is not co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercles. The tympanic annulus is smooth. The first finger is longer than the second; the disks are much wider than the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends maximally to a point between the antepenultimate and penultimate subarticular tubercles on the fourth toe and a point between the penultimate and distal subarticular tubercles on the fifth toe. The dorsum is tan or green, with brown spots or blotches. Markings on the head consist of a dark canthal stripe, and a suborbital spot in some individuals. A pale dorsolateral stripe is absent. The flanks are tan, with diagonal brown bars. The venter is white.

Among the species of *Gastrotheca* in eastern and southeastern Brazil, *G. microdiscus* is most like *G. ernestoi* and *G. fulvorufa*, but *G. microdiscus* has a distinctly long first finger and thereby differs in the relative lengths of the fingers from *G. ernestoi* and *G. fulvorufa*, in which the first finger is equal in length to or only slightly longer than the second. These two species also differ from *G. microdiscus* by having basal webbing between the outer toes; *G. ernestoi* differs further by lacking an inner tarsal fold, and *G. fulvorufa* differs by having prominent tubercles ventrolateral to the cloacal opening. The much larger *G. fissipes*, *megacephala*, *prasina*, and *recava* differ from *G. microdiscus* by having casqued co-ossified heads, and Finger I much longer than Finger II. The same relative finger lengths also are present in *G. albolineata*, *flamma*, and *pulchra*; the former differs from *G. microdiscus* by being green, with a prominent white postorbital stripe. *G. flamma* and *G. pulchra* differ from *G. microdiscus* by having calcars on the heels and one or two tubercles on the outer edges of the upper eyelids, features not present in *G. microdiscus*.

Description

The following description is based on 11 specimens. The body is moderately robust. The maximum snout–vent length is 66.9 mm in males; the largest female has a snout–vent length of 58.8 mm. The head is slightly wider than long, and nearly as wide as the body. The snout is acutely rounded in dorsal view, and is bluntly rounded in profile. The canthus rostralis is rounded in cross-section. The loreal region is shallowly concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 1.5 times the width of the upper eyelid. The internarial area is flat. The nostrils barely protrude laterally at a point slightly posterior to the anterior terminus of the canthus rostralis at a level well posterior to the anterior margin of the lower jaw. The diameter of the eye is notably less than its distance from the nostril. The tympanum is vertically elliptical, and is separated from the eye by a distance about equal to the length of the tympanum. The tympanic annulus is distinct, and is smooth to weakly granular. The supratympanic fold is narrow and granular, barely obscuring the upper edge of the tympanic annulus.

The arm is moderately robust, and lacks ulnar tubercles. The hand is moderate in size. The fingers are long, and bear moderately large round discs; the width of the disc on the third finger is about equal to the length of the tympanum. The relative lengths of the fingers are I > II < IV < III. The fingers are unwebbed. The subarticular tubercles are low and round; none are bifid; the supernumerary tubercles are barely discernible, and are present only on the proximal digits. The palmar tubercle is small and bifid. The prepollical tubercle is robust and ovoid; nuptial excrescences are absent. The hind limbs are moderately slender. The tibia length is slightly more than 50% of the snout–vent length, and is slightly longer than the length of the foot. A calcar and tarsal tubercles are absent; an inner tarsal fold is present on the distal one-fourth of the tarsus. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is ovoid, elevated, and barely visible from above. The toes are long. The relative lengths of the toes are I < II < III = V < IV. The toes are about two-fifths webbed; the webbing formula is **I**2—2½**II**(2—3–3^{+})**III**(2–3)—(2–3^{-})**IV**(2–3)—(2–3) **V**. The subarticular tubercles are large, round, and elevated; supernumerary tubercles are small, and are present only on the proximal segments.

The skin on dorsum of the head, body, and limbs is smooth in females, and is granular in adult males. The skin on the flanks is weakly areolate; the skin on the belly and posteroventral surfaces of the thighs is coarsely granular; the other ventral surfaces are smooth. Cloacal tubercles and folds are absent. The opening of the brood pouch is broadly U-shaped, with the anterior margin at the level of the sacrum. The dentigerous processes of the vomers are posteromedially inclined, and are narrowly separated medially between the round choanae. Each process bears five to seven teeth.

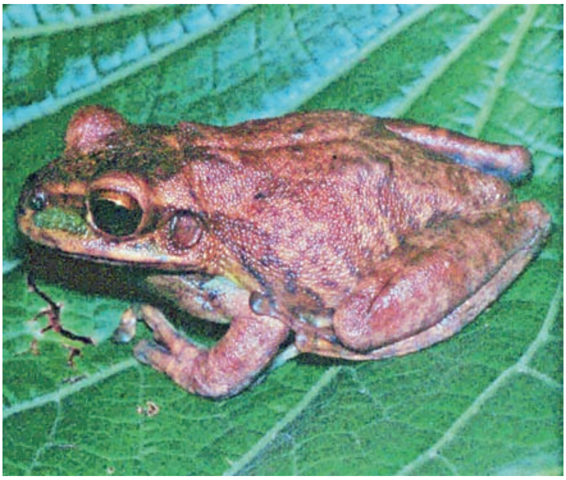

Fig. 10.48 *Gastrotheca microdiscus* (CFBH 11541), female, Pilar do Sul, São Paulo, Brazil. Photo by C. F. B. Haddad, KUDA.

COLOR IN PRESERVATIVE

The dorsum is pale brown, with dark brown to black irregular spots. Dark canthal and postorbital stripes are present. In some individuals the margin of the upper lip is dark brown. Supracloacal stripes are absent; the cloacal region is dark brown to black. The flanks are uniformly creamy tan, with diagonal bars. The anterior and posterior surfaces of the thighs are uniformly pale tan; the venter is uniformly creamy white. Darker brown transverse bars are present on the dorsal surfaces of the limbs: one or two on each forearm and thigh, and three on each shank and foot.

COLOR IN LIFE

I have not observed living individuals of this species. According to Andersson (*in* Lönnberg and Andersson, 1910), the dorsum is green, with black-edged brown spots. A color image of an adult from Pilar do Sul, São Paulo (CFBH 11541) reveals a reddish-tan dorsum with reddish-brown markings, a green loreal region, a tint of dark blue on the hidden surfaces of the shanks, and a reddish-brown iris (Fig. 10.48).

MEASUREMENTS

Females are slightly larger than males. The greater head width in females is reflected in greater internarial and interorbital distances, but not in eyelid width (Table 10.15).

CRANIAL OSTEOLOGY

The sphenethmoid and skull table bear a homogeneous pattern of coarse pit-and-ridge dermal sculpturing. The nasals articulate medially, but are independent of one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each has a wide supraorbital flange and a moderate-sized otic flange. The temporal arcade is incomplete. The frontoparietal covers the anterior epiotic eminence and the anterior part of the posterior eminence, but is not fused with either part; therefore the carotid canal is open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for more than 75% of the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has only a narrow overlap with the dental process of the premaxilla. The quadratojugal is short. The head of the squamosal bears a narrow crest. Owing to the poor condition of the specimen, these are the only characters that could be determined.

Life History

Gastrotheca microdiscus has a few large eggs that undergo direct development. Two females contained only four and five eggs, respectively, in the pouch; it is unlikely that these eggs constituted the entire clutch.

Advertisement Call

Characteristics of the calls of three males recorded in the Atlantic Coastal Forest in the state of São Paulo, Brazil, revealed the following values: notes per call 1,

Table 10.15 Univariate statistics for adults of *Gastrotheca microdiscus*

	Males ($n = 8$)			Females ($n = 3$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	51.9	45.5–66.9	7.76	53.3	48.5–58.8	5.19
Tibia length	26.3	23.0–33.2	3.93	29.1	26.7–31.7	2.50
Foot length	23.7	19.2–31.5	4.65	25.6	22.0–28.8	3.41
Head length	18.9	16.7–23.1	2.72	20.0	16.6–21.3	1.35
Head width	19.1	16.8–24.6	2.92	20.8	20.0–22.0	1.08
Interorbital distance	7.8	6.0–10.5	1.63	7.7	7.5–7.8	0.17
Eyelid width**	4.8	3.7–5.8	0.69	3.9	3.0–5.4	1.31
Internarial distance	4.4	3.8–5.3	0.47	4.4	4.0–5.2	0.67
Eye diameter	5.5	4.5–6.7	0.68	5.4	4.9–5.8	0.47
Eye–nostril distance	5.9	4.5–7.6	1.25	6.0	5.7–6.3	0.30
Orbit–jaw distance	2.8	2.2–3.2	0.35	3.2	2.9–3.5	0.42
Nostril–jaw distance	4.0	3.4–5.0	0.63	4.5	3.9–5.0	0.78
Tympanum diameter	3.3	2.9–3.90	0.37	3.6	3.2–3.9	0.35
Thumb length**	11.2	10.0–13.2	1.51	12.2	11.3–13.0	1.20
Third finger length	17.6	14.4–21.8	3.25	18.6	17.7–19.5	1.27
Disc width	2.6	2.0–3.6	0.59	2.9	2.6–3.2	0.42

**Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

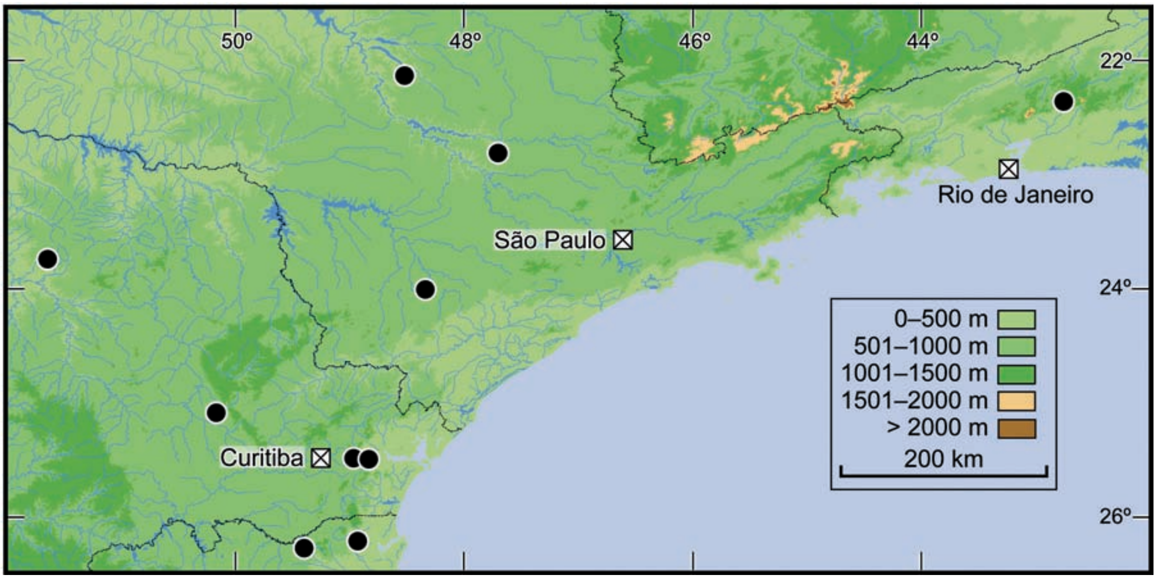

Fig. 10.49 Southeastern Brazil, showing the localities of known occurrences of *Gastrotheca microdiscus*.

2, or 3; duration of first note 124–265 milliseconds; frequency amplitude 0.83–2.38 kHz; dominant frequency 1.38–1.72 kHz; number of pulses 10–38 (Antunes and Haddad, 2009). The authors noted the similarity of the call of this nocturnal frog to that of the diurnal Bare-throated Bellbird (*Procnias nudicollis*) that vocalizes in the same forest as does *Gastrotheca microdiscus*. The duration of the notes of the bellbird generally are longer (185–898 milliseconds) and the frequency amplitude is slightly less (0.95–2.14 kHz) than *G. microdiscus*; the mean dominant frequencies and number of pulses are about identical. These authors queried: convergent evolution or mimicry?

Distribution and Ecology

This species occurs in the Serra do Mar and Serra de Mantiqueira from southern São Paulo to Santa Catarina in southeastern Brazil (Fig. 10.49). A record for Paraguay is highly questionable. The limited information on this species indicates that it inhabits humid forests.

Conservation Status

In the IUCN Red List, *Gastrotheca microdiscus* is categorized as being of Least Concern, "in view of its wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category." Inasmuch as this assessment dates from 2004, its recognition of the species "*G. microdiscus*" includes *G. ernestoi* and *G. fulvorufa*.

Etymology

The specific name is derived from the Greek *mikros*, meaning "small," and the Greek *diskos*, meaning "disk." The name was applied to the size of the terminal discs on the digits, which Andersson (*in* Lönnberg and Andersson, 1910) considered to be small. Caramaschi and Rodrigues (2007) showed that Cochran (1955) and Duellman (1984) were incorrect in their usage of the Latin ending *a* (instead of *us*) in *G. microdisca*, because Andersson (*in* Lönnberg and Andersson, 1910) used the specific name as a noun in apposition.

Remarks

Duellman (1984) analyzed variation in "*Gastrotheca microdisca*" and considered *Nototrema fulvorufa* Andersson, 1911, and *G. ernestoi* Miranda-Ribeiro, 1920, to be junior synonyms. Caramaschi and Rodrigues (2007) re-evaluated the Brazilian *Gastrotheca* and recognized *G. ernestoi* and *G. fulvorufa* as valid species.

Subgenus *Opisthodelphys* Günther, 1859

Opisthodelphys Günther, 1859:117. Replacement name for *Notodelphys* Lichtenstein and Weinland, 1854:373.

Definition

In the large species placed in this subgenus, the tibia length is 50%–55% of the snout–vent length. The head is large, with its width up to 40% or more of the snout–vent length. The interorbital area is broad, more than twice the width of the upper eyelid. The skin is partially co-ossified with the underlying dermal elements of the skull. A prominent transverse occipital ridge bears blunt projections dorsally. There are no striking osteological characters that distinguish this subgenus from its sister taxa *Australotheca* and *Edaphotheca*. The combination of characters is unique among marsupial frogs and, as noted elsewhere in this account, *Gastrotheca ovifera* is singularly distinguished by a row of bony projections across the occiput of the skull.

Reproduction

The eggs undergo direct development and hatch as froglets.

Distribution

This subgenus is restricted to the Cordillera de la Costa and the Sierra de Aroa in northern Venezuela.

Content

One species.

Etymology

The name is derived from the Greek *opisthos*, meaning "behind," and the Greek *delphys*, meaning "womb." The name refers to the brood pouch.

Remarks

In the phylogenetic arrangement proposed by Wiens et al. (2007), *Gastrotheca ovifera* was placed as an outgroup to the Andean species in the genus, but only one gene (16S) of the five genes was included in the analysis. Blackburn and Duellman (2013) did not include *G. ovifera* in their analysis, which was based on four genes. In the analysis presented here, another gene (ND1) was extracted from the only known tissue, collected by the author in 1974. Herein, *G. ovifera* is retained as the subgenus *Opisthodelphys*, a long-branch sister taxon to the Andean *Gastrotheca* of the subgenera *Duellmania*, *Edaphotheca*, and *Gastrotheca*.

Gastrotheca (*Opisthodelphys*) *ovifera* (Lichtenstein and Weinland)

Notodelphys ovifera Lichtenstein and Weinland, 1854:373.—Holotype: ZMB 3073 from Puerto Cabello, Estado de Carabobo, Venezuela.

Notodelphys dorsigera Schlegel, 1858:59.—Holotype: unknown, of unknown provenance. Synonymy fide Nieden, 1923:323.

Nototrema oviferum—Boulenger, 1882:428.

Nototrema oviferum—Nieden, 1923:323.

Hyla vogli Müller, 1938:284.—Holotype: ZSM 67/37 from mountains near Maracay, Venezuela. Synonymy fide Rivero, 1961:143.

Gastrotheca ovifera—Beebe, 1946:193; Rivero, 1961:143.

Gastrotheca (*Opisthodelphys*) *ovifera*—Dubois, 1987:31.

Diagnosis

This large species attains a maximum snout–vent length of 83.0 mm. The tibia length is less than 60% of the snout–vent length, slightly longer than the foot. The interorbital distance is more than twice the width of the upper eyelid. The skin on the dorsum is smooth, and lacks transverse ridges; it is adherent to and partially co-ossified with the skull, which has dorsal projections in the occipital region. Supraciliary processes are absent. The heel usually bears a small tubercle. The tympanic annulus is smooth. The first and second fingers are equal in length. The discs on the fingers are much wider than the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends maximally to the penultimate subarticular tubercle on the fourth toe and the distal subarticular tubercle on the fifth toe. The dorsum is brown, with a narrow dark brown middorsal mark. Markings on the head consist of a pale suborbital bar and dark interocular bar. A pale dorsolateral stripe is absent. The flanks are brown, with vertical black bars in the groin; the venter is dark brown.

Gastrotheca ovifera is readily distinguished from all other members of the genus by three unique characters: dorsal projections in the occipital region of the skull, vertical black bars in the groin, and a dark brown venter.

Description

The following description is based on 52 specimens. The body is robust. The maximum snout–vent length is 57.8 mm in males, and 83.0 mm in females. The head is slightly wider than long, and as wide as the body. The snout is bluntly rounded in dorsal view, and is inclined from the nostrils to the tip in profile. The canthus rostralis is elevated, and is angular in cross-section. The loreal region is deeply concave; the lips are flared. The top of the head is depressed. The interorbital distance is more than 200% of the width of the upper eyelid. The internarial area is slightly depressed. The nostrils are not protuberant, and are directed anterolaterally at a point below the anterior terminus of the canthus rostralis and well posterior to the anterior margin of the lower lip. The diameter of the eye is slightly less than its distance from the nostril. The tympanum is round, and is separated from the eye by a distance about 1.5 times the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is incorporated into the bony squamosal shelf; it projects laterally, obscures the upper part of the tympanum, and extends to a point above angle of the jaw.

The moderately robust arm lacks ulnar tubercles. The hand is moderate in size. The moderately long fingers bear large round discs; the width of the disc on the third finger is greater than the length of the tympanum. The relative lengths of the fingers are I = II < IV < III. The fingers are unwebbed. The subarticular tubercles are large and round; none are bifid. The supernumerary tubercles are round, and are numerous proximally. The palmar tubercle is diffuse; the prepollical tubercle is elliptical; the thumb bears a brown nuptial excrescence in breeding males. The hind limb is moderately slender. The tibia length is about 53% of the snout–vent length; the foot length is about 46% of the snout–vent length. A small tubercle usually (96%) is present on the heel; tarsal tubercles are absent, but a low inner tarsal fold is present on the distal one-fourth of the tarsus. The inner metatarsal tubercle is elliptical, and is not visible from above; the outer metatarsal tubercle is small and subconical. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. The toes are about one-half webbed; the webbing formula is **I**(2^-–2^+)—(2^-–2)**II**(1^+–2^-)—(2½–3^-)**III**(1^+–2^-)—3^-**IV**2½)—(1^+–1½)**V**. The subarticular tubercles are large and round; the supernumerary tubercles are small, subconical, and present only on the proximal segments.

The skin on the dorsum of the body and limbs and on the flanks is smooth; the skin on the head is rugose, and adherent to and partially co-ossified with the underlying cranial elements in adults; the skin on the throat, belly, and posteroventral surfaces of the thighs is coarsely granular; the other ventral surfaces are smooth. The head is casqued, with prominent canthal ridges that are continuous with the supraorbital and supratemporal ridges. A transverse occipital ridge is absent; instead, there are four blunt dorsal projections on the posterior edge of the skull: two parasagittally in the occipital region, and one at the terminus of each supratemporal ridge. Cloacal folds and tubercles are absent. The opening of the brood pouch is elongately and narrowly V-shaped, with its anterior margin at the level of the anterior edge of the sacrum. The dentigerous processes of the vomers are transverse, and are narrowly separated medially at the level of the posterior margins of the choanae. Each process bears six to nine teeth.

Color in preservative

The dorsum is gray to reddish brown, usually (96%) with a narrow dark brown mark extending from the occiput to the sacrum; the mark is bifurcate anteriorly in 40% of the specimens. Dark flecks are scattered on the dorsum in 48% of the specimens. A broad dark brown postorbital mark curves downward onto the anterior part of the flank. The flanks are dark brown to reddish brown, with darker brown to black vertical bars in the groin. The dorsal surfaces of the limbs are colored like the dorsum, with distinct dark brown transverse bars;

usually these are continuous with the bars on the anterior surfaces of the thighs. The posterior surfaces of the thighs are dark brown, with darker brown or black spots (94%) or vertical bars (6%). A pale labial stripe and dark canthal stripe are absent. There usually (94%) is one pale suborbital bar; a dark brown interorbital bar usually (92%) is present. There is no dark patch in the cloacal region; a supracloacal stripe usually (67%) is absent; pale subcloacal spots are absent. The venter is either uniformly dark grayish brown (88%), uniformly pale brown (3%), or pale brown with dark spots (6%). The outer toes are colored like the inner ones.

COLOR IN LIFE

Little variation, except ontogenetically, has been noted in colors of living individuals (Fig. 10.50).

KU 166760, from Rancho Grande, Estado de Aragua, Venezuela.—This adult female is reddish tan above, with chocolate-brown markings on the dorsum, flanks, and outer surfaces of the limbs. The flanks and anterior and posterior surfaces of the thighs are creamy tan, with darker markings. The venter is grayish brown, with darker mottling; the throat is darker than the rest of the venter. The iris is copper, with fine black reticulations (W. E. Duellman field notes, 2 August 1974).

KU 166762, from Rancho Grande, Estado de Aragua, Venezuela.—This juvenile has a tan dorsum, with faintly darker markings. The flanks and thighs are yellowish tan, with black bars; the belly is pinkish gray. The iris is reddish copper (W. E. Duellman field notes, 5 August 1974).

MEASUREMENTS

In most measurements, females are significantly larger than males (Table 10.16).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous fine pit-and-ridge pattern. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange, and has an otic flange that articulates with the head of the squamosal to form a complete temporal arcade. The frontoparietal covers the entire otic region, including the epiotic eminences to which it is fused; hence the carotid canal is closed, and exits the skull posteriorly adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at an angle between 31° and 45°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for more than three-fourths the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The postorbital process of the maxilla is massive, and has a broad diagonal articulation with the wide zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the otic ramus completely articulates with and moderately overlaps the ossified crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in size, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has a blunt terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is separated from the prootic by cartilage. The neopalatines are moderately separated medially; each bears a ventral flange. The pterygoid articulates with the medial side of the zygomatic ramus of the squamosal via an acuminate recurved dorsal ramus on the anterior ramus of the pterygoid. The vomers bear moderately large dentigerous processes located between the middle quadrants of the choanae.

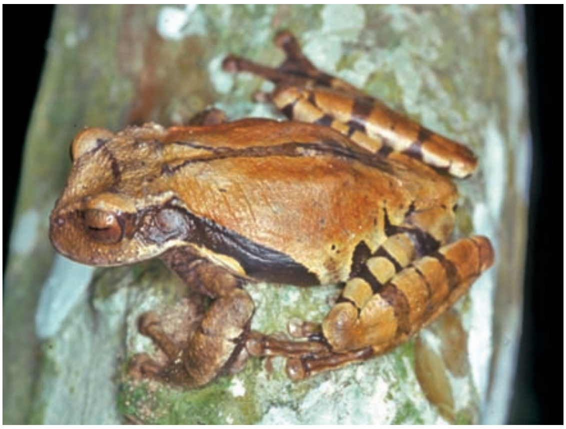

Fig. 10.50 *Gastrotheca ovifera* (KU 166760), female, 75.2 mm SVL, Estación Biológica Rancho Grande, 1100 m, Aragua, Venezuela. Photo by W. E. Duellman.

Life History

At Rancho Grande in the Cordillera de la Costa in Venezuela, *Gastrotheca ovifera* was heard calling from

Table 10.16 Univariate statistics for adults of *Gastrotheca ovifera*

	Males ($n = 4$)			Females ($n = 20$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length**	54.6	50.2–57.8	3.35	68.6	51.3–83.0	10.17†
Tibia length**	28.0	26.8–29.8	1.30	36.9	25.5–44.2	6.03†
Foot length**	24.6	23.1–26.0	1.49	31.8	22.6–39.2	5.01
Head length**	18.8	16.8–20.1	1.42	24.5	17.2–29.8	4.12†
Head width**	21.9	20.6–23.4	1.23	28.3	20.8–34.3	4.36†
Interorbital distance**	8.2	6.9–9.0	0.91	11.7	7.5–14.6	2.16
Eyelid width	4.2	3.7–4.5	0.37	4.3	3.7–5.1	0.45
Internarial distance*	3.4	2.8–3.9	0.46	4.2	2.8–5.0	0.64
Eye diameter	6.2	5.6–6.9	0.56	6.6	5.2–8.4	0.94
Eye–nostril distance*	5.5	4.8–6.7	0.88	7.0	5.0–9.0	1.10
Orbit–jaw distance**	3.1	2.8–3.5	0.31	3.8	2.5–5.8	0.84†
Nostril–jaw distance**	3.9	3.5–4.2	0.35	5.2	3.5–6.9	0.94
Tympanum diameter	3.3	3.0–3.6	0.25	3.8	2.7–4.9	0.56
Thumb length*	10.2	9.5–12.3	1.38	13.6	9.4–16.9	2.33
Third finger length*	19.3	17.7–22.3	2.06	24.1	16.6–30.5	4.14
Disc width	3.7	3.2–4.4	0.50	4.5	3.5–5.7	0.85

*Differences between the means of the sexes are significant (ANOVA, $P = 0.05$).

**Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

†Variances are non-homogeneous (Brown-Forsythe test, $P \leq 0.05$).

7 January until 8 March; brooding females were found from 28 March until 22 May, and the birth of young was observed from 11 May until 3 June (Duellman and Maness, 1980). Mertens (1957) observed breeding in captive individuals from the same locality. He noted that during amplexus, the female raised the posterior part of her body by extending the hind limbs; in this position, with the amplectant pair tilted head down, eggs were extruded from the cloaca. The eggs moved by gravity to the pouch, unassisted by the male. Presumably the eggs were fertilized as they entered the pouch, because the cloaca of the male was positioned just posterior to the opening of the pouch. The eggs hatch as froglets. In observations of parturition of the young by four females, the froglets emerged from the pouch head first, without aid by the female; parturition of 20–43 young ($\bar{x} = 30.7$) required about 5 hours (Duellman and Maness, 1980).

Three preserved females contained eggs in the brood pouch. One, having a snout–vent length of 58.5 mm, contained 27 eggs that were each 11.0 mm in diameter; one (73.8 mm in snout–vent length) contained 20 eggs, 11.3 mm in diameter; and another (74.2 mm in snout–vent length) contained 34 eggs, 6.5 mm in diameter. The holotype, with a snout–vent length of 83 mm, contained 11 eggs in the pouch. One female (EBG 7) has 19 young having snout–vent lengths of 16.9–17.8 mm ($\bar{x} = 17.4$) associated with it.

Advertisement Call

The call consists of two short low-pitched notes, repeated at a rate of two or three calls per minute, with intervals of several minutes between calls.

Distribution and Ecology

Gastrotheca ovifera occurs in the Cordillera de la Costa in northern Venezuela and the Sierra de Aroa to the west (Fig. 10.51). The type locality, Puerto Cabello, is on the Caribbean coast; probably this represents the point of shipment of the specimen, rather than its collection site. A record for the "Delta del Río Orinoco" (MHNLS 2942) undoubtedly is erroneous (Valera-Leal et al., 2011). *G. ovifera* may occur in the Península de Paria; Schargel et al. (2005) reported hearing *Gastrotheca* calling from high in the trees at Cerro Humo in the Península de Paria, Estado de Sucre, in June 2002. The species is known to inhabit cloud forest at elevations of 1050–2000 m. Most individuals have been found on branches of bushes and trees at night, but both juveniles and adults have been found in arboreal bromeliads by day.

Conservation Status

Although *Gastrotheca ovifera* has been known from several protected areas in Venezuela, in the IUCN Red List it is categorized as Endangered. Valera-Leal et al. (2011), who listed many more specimens than those in

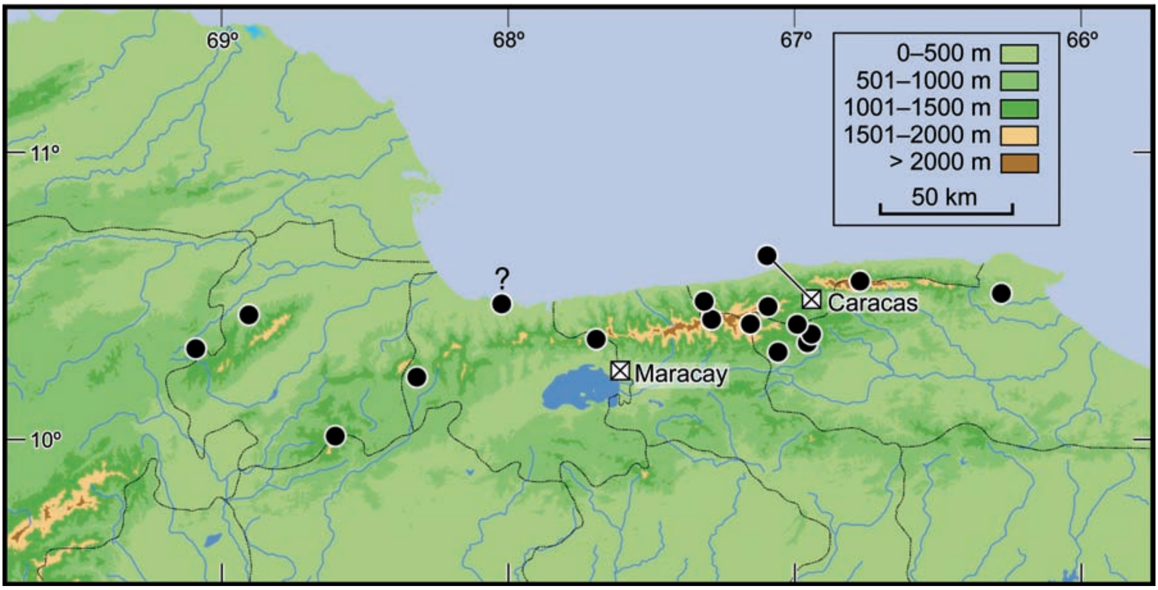

Fig. 10.51 Northern Venezuela, showing the localities of known occurrences of *Gastrotheca ovifera*.

appendix 2, noted that *G. ovifera* had declined in the 1980s and 1990s; their surveys in the Parque Nacional Henri Pittier in 2006 and 2007 revealed no individuals of this species, which previously had been abundant in cloud forest there.

Etymology

The specific name is derived from the Latin *ovum*, meaning "egg," and the Latin suffix *fer*, meaning "carry." The name alludes to the eggs being carried in the pouch.

Remarks

Although Rivero (1961) never examined the holotypes, he was correct in placing *Hyla vogli* Müller, 1938, in the synonymy of *Notodelphys ovifera* Lichtenstein and Weinland, 1854. Although the holotype of *N. ovifera* is soft, it was in good condition when I examined it on 24 July 1969, as was the holotype of *H. vogli*. Somehow Müller (1938) overlooked *G. ovifera* when he described *H. vogli*; both holotypes are in the same collection!

Subgenus *Edaphotheca*, new subgenus

Edaphotheca Duellman.—Type species: *Gastrotheca galeata* Trueb and Duellman, 1978.

Definition

This subgenus contains one medium-sized species with short hind limbs (< 45% of the snout–vent length). The head is barely wider than long. The interorbital distance is about twice the width of the upper eyelid. The skull is casqued and co-ossified. The premaxillae and maxillae are slightly flared anteriorly and laterally, respectively; a low transverse occipital ridge is present. This monotypic subgenus is characterized by a unique combination of cranial osteological features. Chief among these are the depressed snout and the extensive articulation of the maxillae with the premaxillae. The nasals, sphenethmoid, and frontoparietals are heavily synostosed. The otic flanges form a complete temporal arcade, and the carotid canal is partially closed. The lack of a reinforced jaw articulation in this otherwise heavily casqued and co-ossified frog is curious, as is the reduction in the dentigerous processes of the vomer.

Reproduction

The eggs undergo direct development and hatch as froglets.

Distribution

This subgenus is known only from the Huancabamba Depression in northern Peru.

Content

One species.

Etymology

The name is derived from the Greek *edaphos*, meaning "bottom," "foundation," or "base," and the Greek *theke*, meaning "container." The name refers to the phylogenetic position of this subgenus with respect to the Andean subgenera *Duellmania* and *Gastrotheca*.

Remarks

In the earlier molecular phylogenetic analyses by Wiens et al. (2007) and Blackburn and Duellman (2013) and in the more inclusive analysis presented in chapter 3, one species, *Gastrotheca galeata*, appears as a sister taxon to the large Andean clades, recognized herein as the subgenera *Duellmania* and *Gastrotheca*.

Gastrotheca (*Edaphotheca*) *galeata* Trueb and Duellman

Gastrotheca galeata Trueb and Duellman, 1978:498.—Holotype: LSUMZ 32058 from 15 km [by road] east of Canchaque, 1740 m, Región de Piura, Peru.

Gastrotheca (*Opisthodelphys*) *galeata*—Dubois, 1987:31.

Diagnosis

Adults of this medium-sized species attain a snout–vent length of 59.4 mm. The tibia length is less than 45% of the snout–vent length, and is about as long as the foot. The interorbital distance is about twice the width of the upper eyelid. The skin on the dorsum is smooth; it is co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The skin covering the tympanic annulus is smooth. The first finger is longer than the second. The discs on the fingers are slightly wider than the digits. The fingers are unwebbed; on the foot the webbing extends maximally to a point proximal to the antepenultimate subarticular tubercle on the fourth toe and the antepenultimate subarticular tubercle on the fifth toe. The dorsum is tan, with brown paravertebral marks. Markings are absent on the head. A pale dorsolateral stripe is absent. The flanks are tan, with brown spots and mottling; the venter is cream, with brown mottling.

Gastrotheca galeata is distinguished from all other members of the genus by having a co-ossified head, with flared maxillaries and premaxillaries. It also has an elevated transverse occipital ridge, similar to but less prominent than the ridges in other casque-headed species (*G. megacephala*, *nicefori*, and *prasina*). *G. ovifera* also has a casqued head, with prominent dorsal projections on the posterior margin of the skull.

Description

The following description is based on 15 specimens. The body is robust; males attain a snout–vent length of 46.0 mm, and 59.4 mm in females. The head is slightly wider than long. The snout is rounded in dorsal view, and in profile abruptly slopes anteroventrally; it extends well beyond the margin of lower lip. The canthus rostralis is angular in cross-section, and is elevated. The loreal region is deeply concave; the lips are flared. The top of the head is flat. The interorbital distance is about 180% of the width of the upper eyelid. The nostrils are not protuberant, and are directed laterally at the terminus of the canthus rostralis. The diameter of the eye is slightly less than its distance from the eye to the nostril. The tympanum is round, and is separated from the eye by a distance half again the length of the tympanum. The tympanic annulus is distinct; the skin covering the annulus is smooth. The supratympanic fold is massive, co-ossified with the skull, and obscures the upper part of the tympanum.

The arm is moderately robust; ulnar tubercles are absent. The hand is moderate in size. The fingers are unwebbed, and have small round discs; the width of the disc on the third finger is nearly equal to the length of the tympanum. The relative lengths of the fingers are I < II < IV < III. The subarticular tubercles are small and round; none are bifid. The supernumerary tubercles are small, subconical, and numerous on the proximal segments of the fingers. The palmar tubercle is elongate; the prepollical tubercle is elongate, and in males bears a small nuptial excrescence. The hind limbs are robust. The tibia length is 38.6%–44.6% ($\bar{x}$ = 41.7) of the snout–vent length; the foot length is 38.1%–45.2% ($\bar{x}$ = 41.8) of the snout–vent length. Calcars and outer tarsal folds are absent; the inner tarsal fold is straight, and extends the full length of the tarsus. The outer metatarsal tubercle is small and elliptical; the inner metatarsal tubercle is elongate, elevated, and not visible from above. The toes are moderately short. The relative lengths of the toes are I < II< III = V < IV. The toes are less than one-third webbed. Webbing is absent between Toes I–III; the webbing formula for the outer toes is **III**2—(3–3^+) **IV**(3–3^+)—2**V**. The subarticular tubercles are large and subconical; the supernumerary tubercles are small and round.

The skin on the dorsal surfaces of the body and limbs and on the flanks and ventral surfaces of the shanks is smooth; the skin on the head is co-ossified with the underlying bones; the other ventral surfaces are granular. A pair of elliptical tubercles is present below the cloacal opening. The pouch opening is U-shaped, with the anterior border just posterior to the sacrum. The dentigerous processes of the vomers are slightly inclined posteromedially, and are narrowly separated medially between the posterior margins of the small round choanae. Each process bears six to eight teeth.

COLOR IN PRESERVATIVE

The dorsum is tan, with a pair of dark brown paravertebral marks extending from the eyelids to the postsacral region. The facial area is dull brown. Canthal, labial, dorsolateral, and supracloacal stripes are absent. The flanks are tan, with an irregular dark brown stripe extending from the tympanum to the middle of the flank; there are dark brown spots and/or mottling posteriorly on the flanks and on the proximal anterior surfaces of the thighs. The posterior surfaces of the thighs are creamy tan, with expanded dark brown bars. The dorsal surfaces of the limbs have dark brown transverse bars or spots on all segments. The venter is cream, heavily mottled with dark brown.

COLOR IN LIFE

The dorsum is brown, with black markings; the venter is grayish white, mottled with brown; the iris is dull brown (W. E. Duellman field notes, 28 February 1979; Fig. 10.52).

In a juvenile having a snout–vent length of 15.6 mm, the digital discs and ventral surfaces of the limbs were intense reddish orange (E. R. Wild field notes, 7 January 1991).

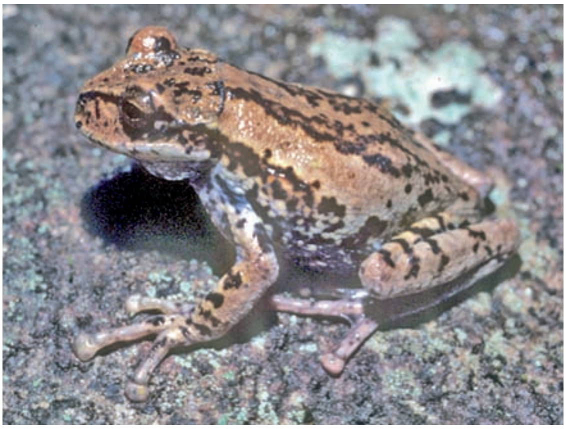

Fig. 10.52 *Gastrotheca galeata* (KU 181700), male, 43.2 mm SVL, 15 km E Canchaque, Piura, Peru. Photo by W. E. Duellman.

MEASUREMENTS

The mean measurements for females are larger than those for males, except for disc width; these differences are significant for 10 measurements (Table 10.17).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in heterogeneous fine pit-and-ridge patterns, with spicules. The nasals articulate medially, and are fused to one another and to the sphenethmoid poste-

Table 10.17 Univariate statistics for adults of *Gastrotheca galeata*

	Males (n = 4)			Females (n = 6)†		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length**	43.6	41.5–46.0	1.86	50.8	48.5–54.8	2.22
Tibia length**	19.0	18.2–20.5	1.09	20.8	19.7–22.6	1.13
Foot length**	19.1	18.0–20.8	1.22	20.9	19.8–21.5	0.57
Head length**	14.3	13.0–15.5	1.12	16.3	15.7–17.2	0.54
Head width**	15.0	14.1–15.7	0.76	16.9	16.3–17.2	0.32
Interorbital distance**	6.8	5.5–6.0	0.70	6.9	6.3–7.5	0.41
Eyelid width	3.3	3.0–3.5	0.24	3.6	3.3–4.0	0.28
Internarial distance**	3.1	2.6–3.5	0.42	3.7	3.4–3.9	0.22
Eye diameter	4.3	4.0–4.6	0.26	4.6	4.5–5.0	0.20
Eye–nostril distance	5.0	4.3–5.7	0.5	5.3	4.8–5.7	0.35
Orbit–jaw distance	2.1	1.8–2.3	0.22	2.4	2.0–3.0	0.41
Nostril–jaw distance	3.0	2.5–3.2	0.33	3.2	3.0–3.3	0.14
Tympanum diameter**	2.6	2.2–2.9	0.29	3.2	2.6–3.5	0.34
Thumb length**	7.4	7.3–7.6	0.15	8.8	8.5–9.2	0.28
Third finger length**	13.9	13.4–15.0	0.76	15.4	14.3–16.6	0.87
Disc width	2.4	2.2–2.6	0.18	2.3	2.0–2.6	0.20

**Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

†The largest female, with a snout–vent length of 59.4 mm, was made into a skeleton before all measurements were taken and thus is not included in this table.

riorly; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange. The otic flange of the frontoparietal is complete to and articulates with the head of the squamosal to form a complete temporal arcade. The frontoparietal covers but is not completely fused to the epiotic eminences; therefore the carotid canal is partially open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a strong angle approximating 45°, thereby resulting in a depressed snout in lateral view. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for more than three-fourths the length of the rostrum. The pars facialis of the maxilla is in contact with the alary process of the premaxilla, and broadly overlaps the dental process of the premaxilla. The quadratojugal is short. The maxilla lacks a distinct postorbital process, but nonetheless has a broad articulation with the massive zygomatic ramus of the squamosal. The head of the squamosal bears a wide crest; the otic plate completely articulates with and moderately overlaps the ossified crista parotica. The dorsal part of the stapedial footplate is more than three times the length of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has an acuminate terminus anterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, where it is separated from the prootic by cartilage. The neopalatines are narrowly separated medially; each bears a ventral flange. The pterygoid lacks a dorsal process on its anterior arm, and thus does not articulate with the medial surface of the zygomatic ramus of the squamosal. The vomers bear minute dentigerous processes located between the posterior quadrants of the choanae.

Life History

Gastrotheca galeata has direct development. Four brooding females collected in December 1974 contained 12, 15, 20, and 24 developing embryos in their pouches.

Advertisement Call

The call is unknown.

Distribution and Ecology

This species is known from elevations of 1720–2130 m on the western slope of the Cordillera Huancabamba in northern Peru (Fig. 10.53). The cordillera, which reaches an elevation of more than 3100 m, forms the continental divide in this part of the Huancabamba Depression. The upper parts of the western slope support cloud forest, whereas the lower slopes are covered with montane dry forest. Localities where *G. galeata* have been found are in the lower part of the cloud forest and in a transition area between the two types of forest. In December 1974, Richard Thomas found males and females by day in crevices between rotting logs and soil in scrubby pasture, and beneath stones in a pasture. On a rainy night in February 1979, a male was climbing a rock cliff in cloud forest. At night in January 1991, three adults and a juvenile were on branches of either bushes or a tree.

Conservation Status

This species is listed as Data Deficient in the IUCN Red List, which states that it is not known to occur in any protected areas, and that further research is needed on this little-known species.

Etymology

The specific name is from the Latin *galea*, meaning "covered with a helmet," and alludes to the casqued head (Trueb and Duellman, 1978).

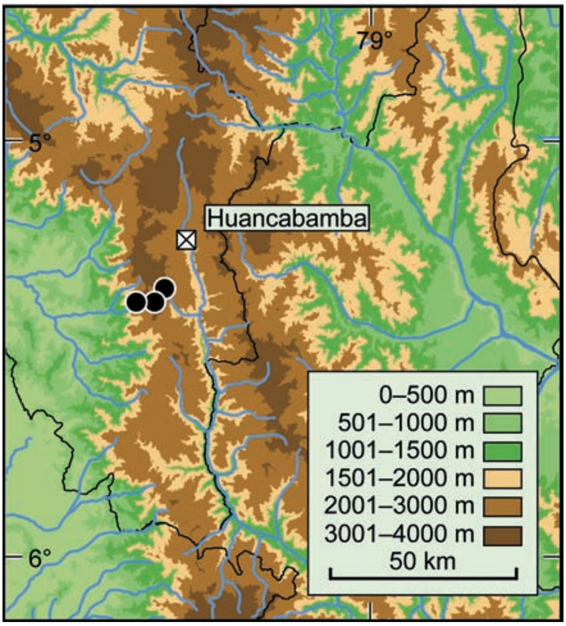

Fig. 10.53 Region of the Huancabamba Depression in southern Ecuador and northern Peru, showing the localities of known occurrences of *Gastrotheca galeata*.

Remarks

The co-ossified head and short robust limbs, with little webbing between the toes, suggest that this species may be fossorial. This idea is corroborated by the limited ecological data; most specimens have been found on the ground or in crevices. In these respects, *Gastrotheca galeata* is unique among the species in the genus.

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11

Andean Species of Subgenus *Duellmania*

As shown in the tree of hypothesized phylogenetic relationships (Fig. 3.1), *Gastrotheca* (*Edaphotheca*) *galeata* is basal to a branch containing two major clades of Andean *Gastrotheca*, which account for about two-thirds of the known species of marsupial frogs. The first clade is treated herein.

Subgenus *Duellmania* Dubois

Duellmania Dubois, 1987:32.—Type species: *Gastrotheca argenteovirens*, by original designation.

Definition

Members of the subgenus *Duellmania* are medium-sized to moderately large (*Gastrotheca nicefori* is large). The skull is not casqued, and the skin on the head is not co-ossified with the underlying cranial elements (co-ossified in *G. nicefori* and *G. trachyceps*). The range of snout–vent lengths in adults is 43–72 mm in males, and 55–73 mm in females. *G. nicefori* is an exception: the largest male has a snout–vent length of 74.7 mm, and the largest female, 81.2 mm. The mean percentage of tibia length to snout–vent length is 47.2%; only five species exceed 50%. The head is wider than long (head width 33.5%–39.5% of the snout–vent length, and head length 31.8%–34.2% of the snout–vent length). All species lack dermal ornamentation. The dorsum is green or brown, usually with a darker middorsal blotch or paravertebral marks.

Osteologically, *Duellmania* is characterized by having moderately deflected alary processes on the premaxillae (much greater in *Gastrotheca ruizi*). Furthermore, all species have a narrow otic plate. In those species for which osteological data exist (*G. lojana*, *monticola*, *orophylax*, and *plumbea*), in the southern clade the neopalatines are widely separated below the sphenethmoid (Fig. 11.1). For additional osteological features, see chapter 4.

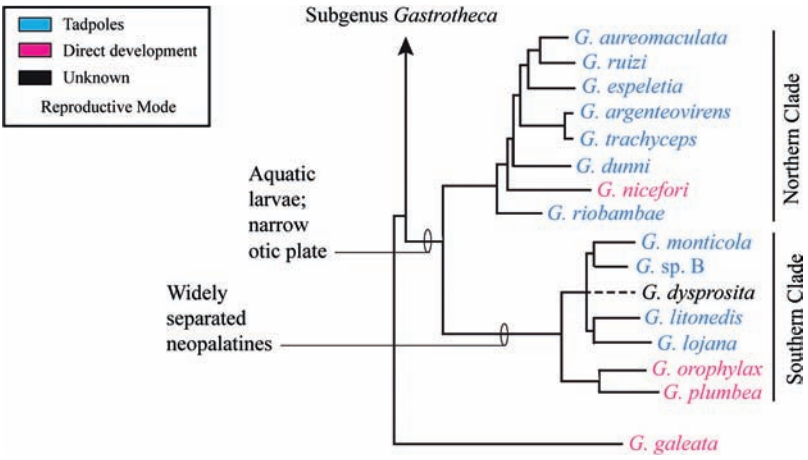
Tadpoles
Direct development
Unknown
Reproductive Mode
Subgenus Gastrotheca
Aquatic larvae; narrow otic plate
Widely separated neopalatines
G. aureomaculata
G. ruizi
G. espeletia
G. argenteovirens
G. trachyceps
G. dunni
G. nicefori
G. riobambae
G. monticola
G. sp. B
G. dysprosita
G. litonedis
G. lojana
G. orophylax
G. plumbea
G. galeata
Northern Clade
Southern Clade

Fig. 11.1 Hypothesized phylogenetic relationships among species of the subgenus *Duellmania*, based on molecular data; the tentative placement of a species lacking molecular data is shown by a dashed line.

Reproduction

In most species the eggs hatch as tadpoles, which complete their development in ponds. The eggs undergo direct development and hatch as froglets in three species: *Gastrotheca nicefori*, *orophylax*, and *plumbea*.

Distribution

Members of this subgenus occur in the Andes from Colombia and Ecuador to extreme northern Peru. Most of the species occur at elevations above 2000 m. One species, *Gastrotheca nicefori*, occurs at lower elevations (800–1600 m) in discrete mountain ranges in Panama, Colombia, and western Venezuela, as well as in the Colombian Andes.

Content

Fourteen species, plus at least one undescribed species.

Etymology

The generic epithet *Duellmania* is a patronym for William E. Duellman.

Remarks

Using data published by other workers, Dubois (1987) recognized numerous subgenera, many of which were new names. Within *Gastrotheca*, he placed all species having direct development in the subgenus *Opisthodelphys*, species having free-living tadpoles and a frontoparietal fontanelle in the subgenus *Gastrotheca*, and species having free-living tadpoles and lacking a frontoparietal fontanelle in the subgenus *Duellmania*. The characteristics and reproductive modes employed by Dubois do not agree with current taxonomy, but the subgeneric names are applicable to monophyletic groups of species.

As shown in the phylogenetic analysis of the family, there are two major clades of *Gastrotheca* that are restricted (or nearly so) to high elevations in the Andes. Of these, *Duellmania* inhabits the northern Andes southward to northern Peru. Two clades are evident in *Duellmania*. In one clade, containing mostly Colombian species that produce tadpoles, the northernmost member of that clade (*G. nicefori*) has eggs that undergo direct development into froglets. In the second clade, containing mostly Ecuadorian species that produce tadpoles, two species (*G. orophylax* and *G. plumbea*) produce froglets. Thus different reproductive modes have evolved twice within *Duellmania* (Fig. 11.1).

KEY TO SPECIES OF *DUELLMANIA*

1. Skin on at least some parts of head co-ossified with underlying dermal bones..........2
   Skin on head not co-ossified with skull; transverse occipital crest absent..........3
2. Skin on head completely co-ossified with underlying cranial elements; transverse occipital crest present; dorsum brown, with or without broad middorsal dark mark; pale dorsolateral stripe absent..........*G. nicefori*
   Skin on head co-ossified with underlying cranial elements only in loreal and postorbital regions; transverse occipital crest absent; dorsum green, with broad paravertebral dark marks; pale dorsolateral stripe present..........*G. trachyceps*
3. Inner tarsal fold absent; snout acutely rounded in dorsal view..........4
   Inner tarsal fold present, at least distally; snout rounded to bluntly rounded in dorsal view..........6

4. Fingers I and II equal in length; interorbital distance much greater than width of eyelid; tympanum golden colored in life.. *G. aureomaculata*
   Finger I slightly longer than Finger II; interorbital distance barely greater than width of eyelid; tympanum not golden colored in life 5
5. Snout short, rounded in profile, extending slightly beyond margin of lip....................................... *G. espeletia*
   Snout long, acuminate in profile, extending well beyond margin of lip... *G. ruizi*
6. Inner tarsal fold extending full length of tarsus........... 7
   Inner tarsal fold present on no more than distal two-thirds of tarsus 10
7. Dorsum green or tan, usually with darker longitudinal paravertebral marks 8
   Dorsum green, without darker longitudinal paravertebral marks 9
8. Finger I shorter than Finger II; outer fingers webbed basally; venter cream .... *G. argenteovirens*
   Fingers I and II equal in length; no webbing between outer fingers; venter dull tan or gray........... *G. lateonota*
9. Pale dorsolateral stripe present; snout in profile steeply inclined anteroventrally.................... *G. plumbea*
   Pale dorsolateral stripe absent; snout in profile truncate.. *G. orophylax*
10. Finger I shorter than Finger II 11
    Fingers I and II equal in length....................................... 12
11. Webbing extending to penultimate subarticular tubercle on fourth toe; venter cream, with dark spots .... *G. monticola*
    Webbing extending to antepenultimate subarticular tubercle on fourth toe; venter uniformly cream .... *G. dunni*
12. Webbing extending to penultimate subarticular tubercle on fourth toe .... *G. riobambae*
    Webbing extending to antepenultimate subarticular tubercle on fourth toe 13
13. Tympanic annulus granular; dorsum green, with irregular middorsal yellow stripe................ *G. dysprosita*
    Tympanic annulus smooth; coloration not as described 14
14. Venter uniformly pale brownish gray............ *G. litonedis*
    Venter cream, with dark flecks or irregular markings .... *G. lojana*

Gastrotheca (*Duellmani*) *argenteovirens* (Boettger)

Hyla argenteovirens Boettger, 1892:46.—Lectotype: SMF 2676 (designated by Mertens, 1957:41) from Popayán, Departamento de Cauca, Colombia.
Gastrotheca marsupiata argenteovirens—Mertens, 1933:259.
Gastrotheca monticola argenteovirens—Cochran and Goin, 1970:185.
Gastrotheca argenteovirens—Duellman and Fritts, 1972:7.
Gastrotheca (*Duellmania*) *argenteovirens*—Dubois, 1987:33.

Diagnosis

In this medium-sized species (females to 65.0 mm), the tibia length is less than 55% of the snout–vent length; the tibia is barely longer than the foot. The interorbital distance is about twice the width of the upper eyelid. The skin on the dorsum usually is smooth, not co-ossified with skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a tubercle or calcar; the tympanic annulus is smooth. The first finger is shorter than the second. The discs are much wider than the adjacent digits. The fingers are webbed basally; on the toes, the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and the distal subarticular tubercle on the fifth toe. The dorsum is tan, brown, or green, usually with darker paravertebral marks. A pale labial stripe is present; other markings are absent on the head, but a pale dorsolateral stripe is present. The flanks are either gray, or blue with dark spots; the venter is cream, with dark flecks or spots.

Gastrotheca argenteovirens differs from all other species of the subgenus (except *G. trachyceps*) by having the groin, anterior and posterior surfaces of the thighs, and ventral surfaces of the shanks all be blue, with black spots. It differs from *G. trachyceps* by lacking dermal co-ossification of the skull.

Description

The following description is based on 40 males and 50 females. The body is moderately robust; the maximum snout–vent length is 55.9 mm in males, and 65.0 mm in females. The head is slightly wider than long, and as wide as the body. The snout is bluntly rounded in dorsal view, and is rounded and anteroventrally inclined in profile. The canthus rostralis is rounded in cross-section. The loreal region is barely concave; the lips are rounded. The top of the head is flat. The interorbital distance is about twice the width of the upper eyelid. The internarial area is barely concave. The nostrils are barely protuberant, and are directed anterolaterally at a point below the anterior terminus of the canthus rostralis, slightly posterior to the level of the anterior margin of the lower jaw. The diameter of the eye is about equal to its distance from the nostril, and about twice its distance from the margin of the jaw. The tympanum is round, and is separated from the eye by a distance about equal to its diameter. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately heavy, extends from the posterior corner of the orbit to a point just above the insertion of the forelimb, and obscures the upper edge of the tympanum.

The arm is moderately robust, and lacks ulnar tubercles. The hand is moderate in size. The fingers are moderately long, and are barely webbed basally. The discs are moderately large and round; the width of the disc on the third finger is about equal to the diameter of the tympanum. The relative lengths of the fingers are I = II < IV < III. The subarticular tubercles are small, low, and round; small supernumerary tubercles are numerous on the proximal segments of the digits. The palmar tubercle is low, diffuse, and bifid; the elongately elliptical prepollical tubercle bears brown nuptial excrescences in breeding males. The hind limb is moderately robust. The tibia length is about 50% of the snout–vent length; the foot length is about 47% of the snout–vent length. Calcars are absent; the tarsal tubercles are small and subconical. The inner tarsal fold is curved along the full length of the tarsus. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is ovoid, elongate, and barely visible from above. The toes are moderately long and slender. The relative lengths of the toes are I < II < III < V < IV. The toes are about one-third webbed; the webbing formula is **I**2—2^{+}**II**3^{-}—3**III**2—3**IV**3—(1–2)**V**. The subarticular tubercles are small and round; small supernumerary tubercles are in single rows on the proximal segments of the digits.

The skin on the dorsum is smooth (86%) or granular (14%); the skin on the flanks is areolate; the skin on the throat, belly, and posteroventral surfaces of the thighs is coarsely granular; the other surfaces are smooth. Supraciliary processes are absent on the eyelids. The cloacal sheath is short and granular. The opening of the brood pouch is U-shaped, with the anterior margin at the level of the posterior edge of the sacrum. The dentigerous processes of the vomers are slightly inclined posteromedially, and are narrowly separated medially at the level of the posterior margins of the small round choanae. Each process bears three or four teeth.

COLOR IN PRESERVATIVE

The dorsum is pale brown or bluish gray, with darker paravertebral longitudinal marks (77%), a middorsal dark blotch (11%), and/or dark flecks (85%). Indistinct dark transverse marks on the thighs are present in 11% of the specimens; the dorsal surfaces of the other segments of the limbs are unmarked. A narrow creamy white dorsolateral line extends from the outer margin of the upper eyelid to the groin. A creamy white labial stripe is present in 69%; it extends onto the anterior part of the flank in 36%. The cloacal region is dark brown, bordered above by a bronze or cream transverse stripe in 84%. A narrow cream or bronze stripe is present on the heel in 79%; faint cream stripes are present on the outer edges of the forearms and tarsi in 24%. The flanks are brown or gray, with a variable number of white spots or flecks; the groin is blue, with black spots. The anterior and posterior surfaces of the thighs are blue, with black spots; white flecks are present on the anterior surfaces in some specimens. The chest and belly are cream to pale brown, with dark brown or black flecks or spots; the ventral surfaces of the shanks are mottled bluish gray and black. The vocal sac is gray.

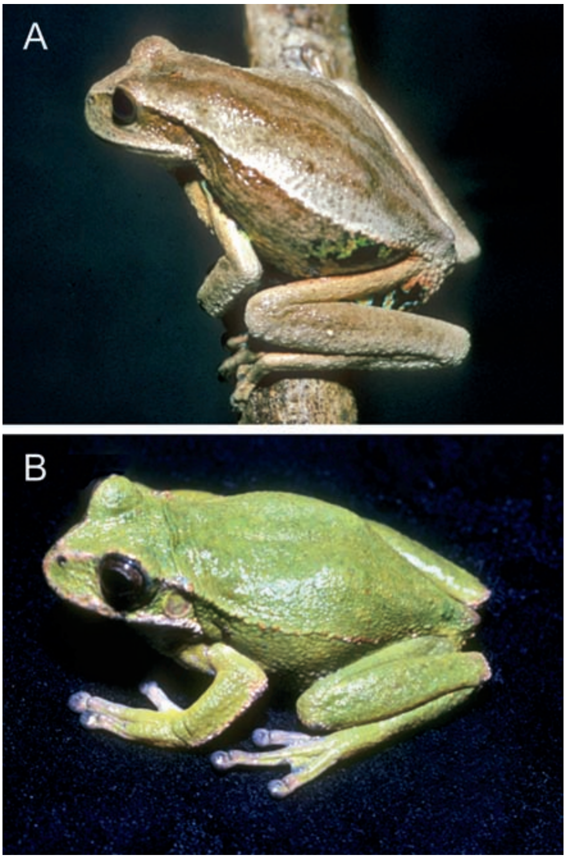

Fig. 11.2 *Gastrotheca argenteovirens*. A: KU 168405, female, 58.6 mm SVL, 7 km NE Tenerife, 2850 m, Valle de Cauca, Colombia. B: KU 181175, male, 53.4 mm SVL, 6 km E Silvia, 2690 m, Cauca, Colombia. Photos by W. E. Duellman.

COLOR IN LIFE

The dorsum varies from tan to brown and green, usually with darker markings (Fig. 11.2). All shades occur in one population, as is evidenced from the color description of specimens from three localities.

KU 169403–11 from 7 km NE Tenerife, Departamento de Valle del Cauca, Colombia.—The dorsum is tan to brown, with black-bordered blue ocelli and dark brown to black flecks; four tan individuals have dark brown longitudinal marks. The dorsolateral, canthal, labial, heel, and ulnar stripes are creamy tan. Both the side of the head posterior to the orbit and the anterior flanks are dark brown. The axilla, ventral surface of upper arm, groin, anterior and posterior surfaces of thighs, ventral surface of shank, and inner surfaces of the feet (including bases of Toes I–IV) are pale blue, with bold black mottling. The upper posterior part of the flank and border of the dorsal color of the thighs are salmon, mottled with black (some with an extensive suffusion of orange to coral on the flanks and hind limbs). The throat and belly are bronze tan to grayish brown, with or without dark brown flecks. The vocal sac and ventral surfaces of the thighs are dull grayish brown. The iris is pale bronze, with black reticulations; the tongue is cream; the lining of the mouth is pale blue (W. E. Duellman field notes, 3–4 June 1976).

KU 181168–73 from 2 km E Silvia, Departamento de Cauca, Colombia.—The dorsum is tan, brown, or green, with faintly darker markings and bronze dorsolateral, labial, tarsal, and cloacal stripes. The belly is tan to creamy tan, with grayish-brown spots. The axilla, groin, anterior and posterior surfaces of the thighs, and the inner surfaces of the shanks and feet are deep blue, with black mottling. Orange spots are present on the flanks in some tan and green individuals, whereas green spots are present on the flanks in brown individuals. The iris is coppery bronze, with fine black reticulations (W. E. Duellman field notes, 21 March 1979).

ICN 7541–55 from 6 km E Totorá, Departamento de Cauca, Colombia.—The basic color is either green or brown. Green frogs have some bronze markings on the head and above the sacrum. The dorsolateral ridge, fingers, and toes are bronze. The iris is bright yellow copper, with black reticulations. The venter is creamy bronze; the axilla, groin, and hidden surfaces of the limbs are blue, with a hint of darker blue spots. In brown frogs, the dorsolateral stripe is cream. The flanks are a darker brown than the dorsum; some green blotching is evident; yellow spots are present in the groin. In both green and brown frogs, a line of pale tubercles extends from below the eye to below the tympanum and onto the upper lip. One brown frog has paravertebral brown stripes; a large green specimen has pronounced dusky gray marbling on the venter (J. D. Lynch field notes, 3 August 1980).

MEASUREMENTS

Females are slightly larger than males (Table 11.1).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous fine pit-and-ridge pattern. The

Table 11.1 Univariate statistics for adults of *Gastrotheca argenteovirens*

	Males (n = 40)			Females (n = 50)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	47.9	41.6–55.9	3.41	55.1	41.8–65.0	5.14
Tibia length	23.4	20.5–27.1	1.68	28.1	21.3–34.8	2.99
Foot length	22.3	18.5–25.6	1.74	26.4	20.6–33.0	2.58
Head length	15.8	13.9–17.7	0.98	17.8	13.2–20.5	1.49
Head width	17.2	15.3–19.9	1.24	19.8	14.8–28.9	2.06
Interorbital distance	5.8	4.6–7.1	0.50	6.8	4.8–9.2	1.11
Eyelid width	3.5	2.4–4.8	0.56	3.4	2.7–5.2	0.61
Internarial distance	3.0	2.4–4.0	0.29	3.4	2.5–5.5	0.46
Eye diameter	4.8	3.9–5.8	0.50	5.2	3.8–7.0	0.60
Eye–nostril distance	4.6	4.0–6.0	0.39	5.3	3.9–6.6	0.52
Orbit–jaw distance	2.3	1.9–2.9	0.24	2.6	1.9–3.1	0.28
Nostril–jaw distance	3.3	2.4–4.7	0.42	3.8	2.9–5.2	0.43
Tympanum diameter	2.7	2.3–3.7	0.31	3.1	1.9–4.2	0.43
Thumb length	8.5	6.8–10.0	0.88	9.9	7.2–12.2	1.19
Third finger length	16.5	14.5–18.9	1.24	19.2	15.3–23.6	1.90
Disc width	2.8	2.2–2.4	0.32	3.2	2.4–4.1	0.37

nasals articulate medially, and are fused to one another; owing to synostosis, the posteromedial borders of the nasals are indistinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange and a small otic flange. A temporal arcade is absent. The frontoparietal covers the anterior epiotic eminence and the part of the posterior eminence to which it is partially fused; thus the carotid canal is closed; there is a small fenestra in the frontoparietal over the canal, in the region of the junction of the epiotic eminences. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae bear long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for about half the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The postorbital process of the maxilla is massive, and has a broad horizontal articulation with the wide zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the otic plate articulates with and narrowly overlaps the crista parotica. The dorsal part of the stapedial footplate is more than three times the length of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified posterior to the midlength of the orbit, but is not synostosed with the prootic. The neopalatines are widely separated medially, and bear a ventral flange. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a long acuminate recurved process on the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located at the posterior margins of the choanae.

Life History

The eggs hatch into tadpoles in Stages 34–37; three clutches of young were born in the laboratory in Bogotá, Colombia, to females collected on 3 August 1980 at 4.5 km E Silvia, Departamento de Cauca, Colombia (Table 11.2). The late Pedro M. Ruíz-C. noted that newly born tadpoles are dark olive green. The tadpoles hatch with well-formed hind limbs, with four or five toes differentiated; two upper and three lower rows of labial teeth are present at birth.

Table 11.2 Development of tadpoles of *Gastrotheca argenteovirens*

	Female catalogue number		
Parameter	ICN 5808	ICN 6311	ICN 6423
Female snout–vent length (mm)	55.5	57.1	56.4
Clutch size	29	20	55
Stage at hatching	35	34	34
Mean body length at birth (mm)	12.3	10.5	10.2
Mean total length at birth (mm)	32.1	25.6	24.5
Mean SVL at metamorphosis (mm)	14.6	14.3	11.7
Duration of larval stages (days)	19–20	26–36	43

Tadpoles

A typical tadpole in Stage 38 (ICN 6417) has a body length of 14.1 mm and a total length of 35.0 mm. In dorsal view the body is ovoid, widest at midlength, and wider than deep; the snout is bluntly rounded. In profile the snout is inclined abruptly from the nostrils to the tip of the snout. The throat is slightly concave. The eyes are widely separated, and are directed dorsolaterally. The nostrils are about midway between the eyes and the tip of the snout. The spiracle is directed posterolaterally at a point about three-fifths the length of the body; the spiracular opening is below the midline. The cloacal tube is median, long, and conical. The caudal musculature is moderately robust; it gradually tapers to a tip just short of the rounded tip of the tail. The dorsal fin arises gradually from the body. The fins are about equal in height; at midlength of the tail, each fin is slightly higher than the caudal musculature. The body and tail are pale gray, with no distinctive markings.

The width of the oral disc is equal to about half the width of the body; the disc is bordered by two alternating rows of short conical papillae laterally and ventrally, and one row anteriorly. There are two upper and three lower rows of labial teeth; the tooth rows are about equal in length; the first lower row is narrowly interrupted medially. The jaw sheaths are moderately robust, and bear short blunt serrations; both jaw sheaths are broadly arch-shaped.

Metamorphosing young have snout–vent lengths of 11.0–14.7 mm ($\bar{x} = 12.9$, $n = 7$). The late Pedro M. Ruíz-C. noted that in two of these the dorsum was pale green, with dark brown markings.

Advertisement Call

The call is a low-pitched "wraaack," followed or not by two or three short notes, "tlack-tlack-tlack."

Distribution and Ecology

This species is widely distributed in the central and southern parts of the Cordillera Central in Colombia, where it occurs at elevations of 2000–2850 m (Fig. 11.3). To the south of the Cordillera Occidental in southern Colombia, the species occurs at elevations of 2650–3050 m in the Nudo de Pasto.

Gastrotheca argenteovirens has been found in subpáramo, cloud forest, and farmland (including potato fields and pastures). By day individuals take shelter in terrestrial bromeliads, in the axils of leaves of large *Agave*, and in rock piles. At night adults have been found on the leaves of *Agave*, on the trunks and low branches of bushes (e.g., *Baccharis*), and on the ground. Tadpoles develop in shallow water in drainage ditches and grassy ponds.

Conservation Status

Although the species is not known to occur in any protected areas, it is listed as being of Least Concern in the IUCN Red List. *Gastrotheca argenteovirens* is abundant in farmland; pesticides may impose a threat to the species in these areas.

Etymology

The specific name is derived from the Latin *argenteus*, meaning "silver," and the Latin *viridis*, meaning "green." The name refers to the bluish-green color in the groin and hidden surfaces of the limbs referred to by Boettger (1892).

Remarks

The type locality, Popoyán, at an elevation of 1760 m, is 240 m lower than any other known locality for the species. This town may have been a central location for material collected by F. Lehmann and shipped to European museums. Prior to Duellman's (1987) review of the species, *Gastrotheca argenteovirens* was thought to occur throughout the Cordillera Central and in the southern part of the Cordillera Occidental in Colombia. Lutz (1977) recognized specimens from the northern part of the Cordillera Central as a subspecies, *G. argenteovirens dunni*. Duellman (1987) provided morphological evidence for the recognition of *G. dunni* as a distinct species; it differs from *G. argenteovirens* in coloration, size, and degree of webbing on the feet. The frogs from the southern part of the Cordillera Occidental were regarded as a distinct species, *G. trachyceps*, principally

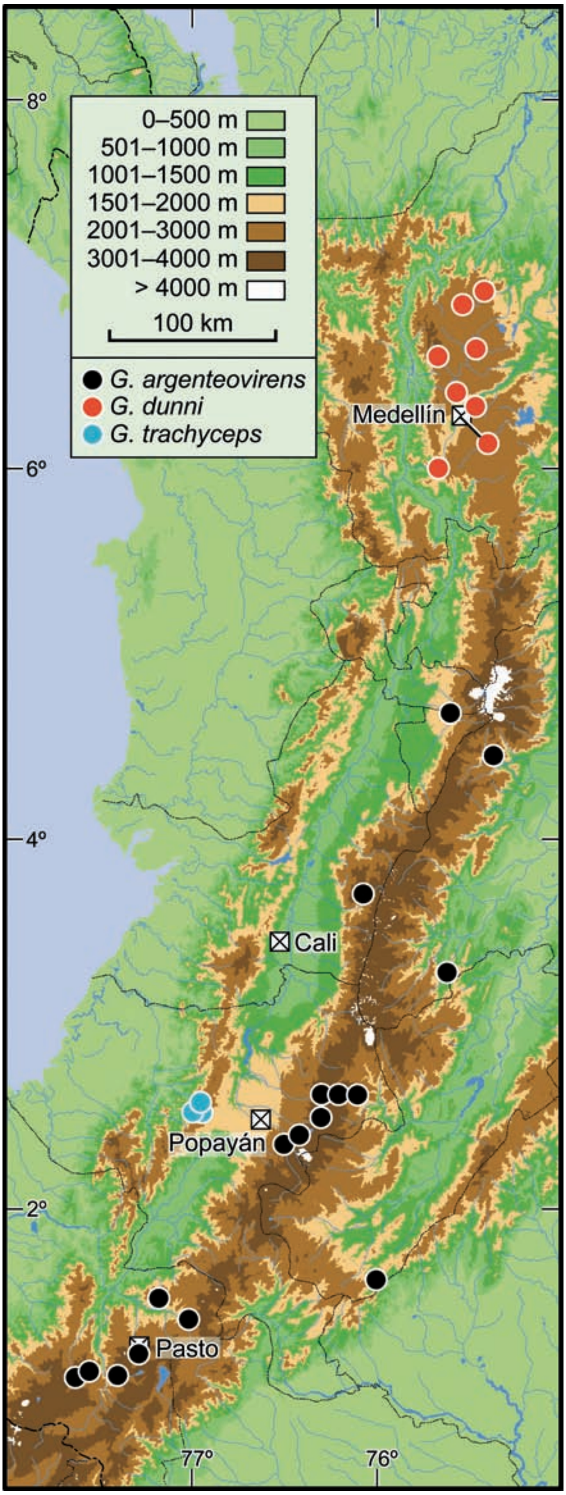

Fig. 11.3 Andean region of Colombia, showing the localities of known occurrences of *Gastrotheca argenteovirens*, *dunni*, and *trachyceps*.

by the occurrence of dermal-cranial co-ossification (Duellman, 1987). Analyses of molecular data show that *G. argenteovirens* and *G. trachyceps* are sister species within a small clade that also includes *G. aureomaculata*, *dunni*, and *ruizi*, all confined to the Andes in Colombia.

Gastrotheca (Duellmania) aureomaculata Cochran and Goin

Gastrotheca aureomaculata Cochran and Goin, 1970:177.—Holotype: FNHM 69701 from San Antonio, ca. 25 km W San Agustín, Departamento de Huila, Colombia.

Gastrotheca mertensi Cochran and Goin, 1970:181.—Holotype: UMMZ 121024 from Moscapán, Departamento de Cauca, Colombia. Synonymy fide Duellman, 1983:109.

Gastrotheca aureomaculata—Duellman, 1983:109.

Gastrotheca (*Duellmania*) *aureomaculata*—Dubois, 1987:33.

Diagnosis

In this large species (females to 75.6 mm), the tibia length is less than 55% of the snout–vent length, barely longer than the foot. The interorbital distance is noticeably greater than the width of the upper eyelid. The skin on the dorsum is areolate or granular, and lacks transverse ridges; the skin on the head is not co-ossified with the underlying cranial elements. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first and second fingers are equal in length, and bear discs that are much wider than the digits. The fingers are unwebbed; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is uniformly green or dark brown, with small pale spots. Markings are absent on the head, or consist of small pale spots. A pale dorsolateral stripe is absent. The flanks are dark brown, with or without pale spots; the venter is gray, with or without small pale spots.

The spotted color phase of *Gastrotheca aureomaculata* is unlike that of any other species of the genus. The dorsal pattern is similar to that of *Hyloscirtus pantostictus* of the Andes of extreme southern Colombia and northern Ecuador, but *Hyloscirtus* has bold dark mottling on the belly, whereas the belly of *G. aureomaculata* is uniformly dull gray or has small pale spots. Green individuals of *G. aureomaculata* can only be confused readily with *G. orophylax*, which differs by having smoother skin on the dorsum and more webbing on the feet, and by lacking a golden tympanum; and *G. carinaceps*, which differs by having an inclined snout in profile, prominent cranial crests, and a green tympanum. Other *Gastrotheca* in the northern Andes that have a green dorsum include *G. argenteovirens* and *G. plumbea*, both of which usually have a pale dorsolateral stripe above the brown (*G. plumbea*) or spotted (*G. argenteovirens*) flanks; neither has a golden tympanum.

Description

The following description is based on 28 individuals. The body is moderately robust; males attain snout–vent lengths of 71.6 mm, and 75.6 mm in females. The head is slightly wider than long, and nearly as wide as the body. The snout is acutely rounded in dorsal view, and is bluntly rounded in profile. The canthus rostralis is angular in cross-section. The loreal region is concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 175% of the width of the upper eyelid. The internarial area is flat. The nostrils are not protruding, and are directed dorsolaterally at a point below the anterior terminus of the canthus rostralis just posterior to the anterior margin of the lower jaw. The diameter of the eye is about equal to its distance from the nostril. The tympanum is round, and is separated from the eye by a distance nearly twice the diameter of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately heavy, and extends from the posterior corner of the orbit to a point above the insertion of the arm.

The arm is moderately robust, and lacks ulnar tubercles. The hand is large. The fingers are long, and bear large round discs; the width of the disc on the third finger is slightly greater than the diameter of the tympanum. The relative lengths of the fingers are I = II < IV < III. The fingers are unwebbed. The subarticular tubercles are moderately large and flat; none are bifid. The supernumerary tubercles are small, round, and present only proximally. The palmar tubercle is low, flat, and bifid; the prepollical tubercle is elliptical, and bears nuptial excrescences in breeding males. The hind limb is robust. The tibia length is about 50% of the snout–vent length; the foot length is about 48% of the snout–vent length. A calcar on the heel, tarsal tubercles, and a tarsal fold are absent. The outer metatarsal tubercle is small and subconical; the inner metatarsal tubercle is small, elevated, elliptical, and not visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. The toes are about two-fifths webbed; the webbing formula is **I**2^{+}—(2–2^{+}) **II**2^{-}—3**III**3—(3–3½)**IV**(3–3½)—2**V**. The subarticular tubercles are large and flat; the supernumerary tubercles are minute, weak, and present only proximally.

The skin on the dorsum of the head, body, and limbs is areolate (43%) or granular (57%); the skin on the flanks is areolate; the skin on the throat, belly,

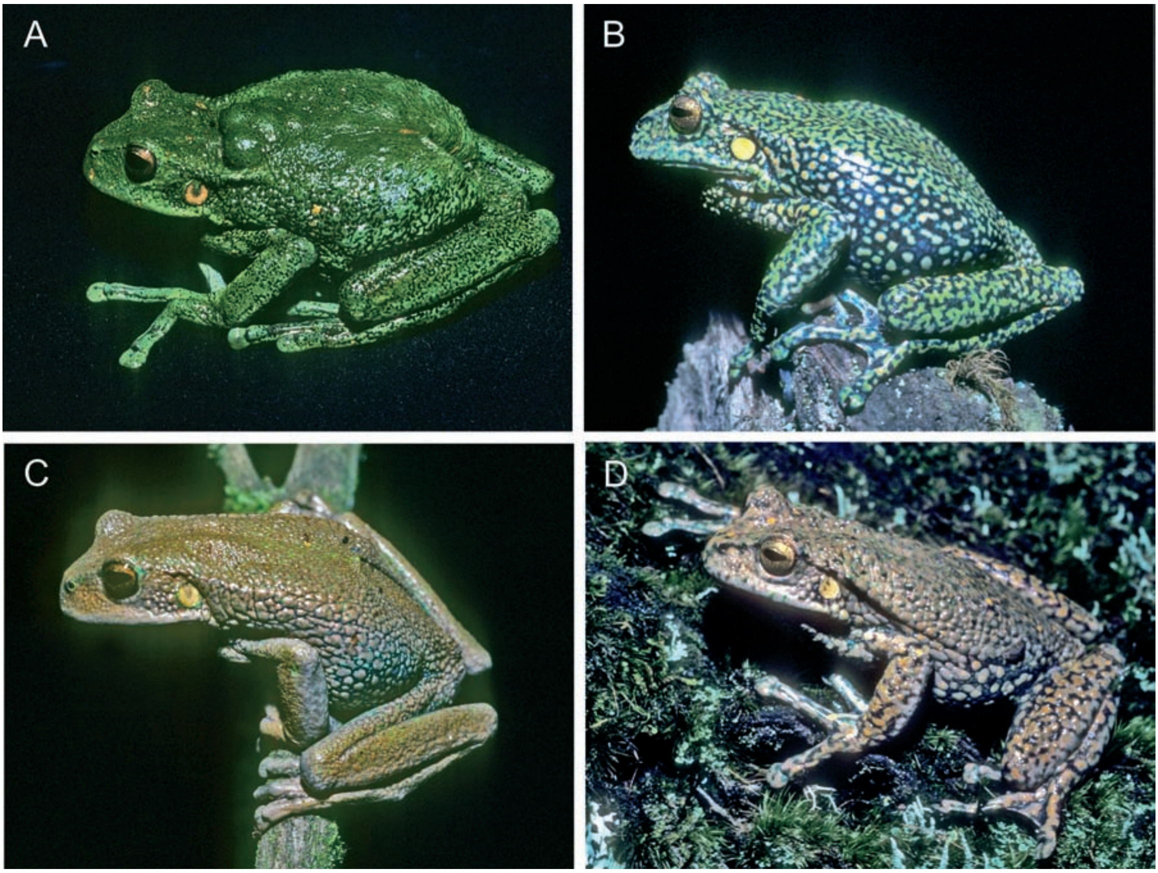

Fig. 11.4 *Gastrotheca aureomaculata*. A: KU 118196, female, 75.4 mm SVL. B: KU 181197, male, 63.7 mm SVL. C: KU 118198, female, 67.5 mm SVL. D: KU 181200, male, 67.9 mm SVL. All from Moscapán, 14.7 km W Leticia, 2050 m, Cauca, Colombia. Photos by W. E. Duellman.

and ventral surfaces of the thighs is granular. Cloacal tubercles and folds are absent. The pouch opening is U-shaped, with the anterior margin at the level of the posterior edge of the sacrum. The vocal sac is large, median, and subgular. The dentigerous processes of the vomers are posteromedially inclined, and are narrowly separated medially between the posterior margins of the small round choanae. Each process bears six or seven teeth.

COLOR IN PRESERVATIVE

Dorsal coloration is polychromatic (Fig. 11.4). The dorsal surfaces of the head and body are either uniformly dull bluish gray (43%) or have pale cream spots (57%); the dorsal surfaces of the shanks are colored like the body, but spotted in only 29% of the specimens. Labial, canthal, dorsolateral, and supracloacal stripes are absent. The tympanum is pale cream. The flanks are uniformly dull gray (29%) or with pale spots (71%); the anterior and posterior surfaces of the thighs are uniformly gray (54%) or have pale spots (46%); and the ventral surfaces are uniformly dark gray (64%) or have pale spots (36%).

COLOR IN LIFE

The coloration in life varies from nearly uniformly green to dark brown (nearly black) with small orange-yellow spots (Fig. 11.4). In all individuals, the tympanum is a deep golden color; a dull blue suffusion is present in the axilla and groin, and on the posterior surfaces of the thighs. The iris is deep bronze, with fine black reticulations.

Nine specimens (KU 181194–202) from Moscapán, Departamento de Cauca, Colombia.—The variation in coloration on the dorsum was brownish black with tan spots (1 specimen), brown or tan with orange-yellow spots (4), green with black flecks (2), green with a brown suffusion middorsally (1), and tan with dark brown reticulations (1). In these frogs the venter was dull tan with varying amounts of black reticulations (5

Table 11.3 Univariate statistics for adults of *Gastrotheca aureomaculata*

	Males ($n = 16$)			Females ($n = 12$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length**	63.4	59.1–71.6	3.94	70.5	62.6–72.6	3.70
Tibia length	31.4	28.9–35.1	1.82	36.5	33.7–39.7	2.11
Foot length	30.3	28.1–33.6	1.64	35.8	33.3–39.8	2.00
Head length**	22.2	19.8–25.7	1.57	23.7	22.7–25.5	0.76
Head width**	23.6	21.2–25.0	1.02	26.4	24.4–28.0	1.09
Interorbital distance	6.3	6.4–8.6	0.55	8.5	7.6–9.5	0.70
Eyelid width	4.6	3.4–5.8	0.70	4.6	2.2–5.9	0.93
Internarial distance	4.3	3.8–5.5	0.43	4.5	4.1–5.5	0.38
Eye diameter	5.9	4.5–7.7	0.84	6.2	4.9–7.8	0.73
Eye–nostril distance	5.8	4.9–6.6	0.41	6.6	5.4–7.1	0.43
Orbit–jaw distance**	3.2	2.7–4.1	0.34	3.8	3.2–4.0	0.40
Nostril–jaw distance**	4.7	3.8–5.8	0.57	5.3	4.5–5.9	0.42
Tympanum diameter	3.5	2.7–4.5	0.51	3.8	3.1–4.5	0.45
Thumb length**	12.1	10.8–13.5	0.73	14.1	13.0–16.2	0.99
Third finger length**	22.4	20.2–25.0	1.24	26.2	22.6–29.6	2.14
Disc width	3.7	2.9–4.4	0.38	4.2	3.6–4.9	0.45

**Differences between the means of the sexes are significant (ANOVA, $P \le 0.01$).

specimens); with cream, tan, or pale green spots (3); or uniformly bluish gray (1) (W. E. Duellman field notes, 21 March 1979).

MEASUREMENTS

The means of all measurements, except six, are significantly larger in females than in males (Table 11.3).

CRANIAL OSTEOLOGY

The sphenethmoid is smooth and superficially unsculptured, although it bears an internal vermiform pattern of ossification; the other bones of the skull table bear a heterogeneous pattern of coarse shallow pit-and-ridge dermal sculpturing. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have an incomplete medial articulation; each bears a narrow supraorbital flange and a small otic flange. A temporal arcade is absent. The frontoparietal covers the anterior epiotic eminence and the anterior part of the posterior epiotic eminence. The frontoparietal is partially fused to the epiotic eminence; therefore the carotid canal is partially closed, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae bear long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for about one-fourth the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The postorbital process of the maxilla is massive, and has a broad diagonal articulation with the massive zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the otic plate articulates with and narrowly overlaps the crista parotica. The dorsal part of the stapedial footplate is more than three times the length of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has a blunt terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are moderately separated medially; each bears a ventral flange. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a long acuminate recurved process on the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located between the middle quadrants of the choanae.

Life History

Gastrotheca aureomaculata broods eggs that hatch as tadpoles. Three brooding females having snout–vent lengths of 72.6–75.mm ($\bar{x} = 6.5$) contained 76–116 eggs

($\bar{x}$ = 101) that had diameters of 5.1–7.5 mm ($\bar{x}$ = 6.5). Cochran and Goin (1970) reported on the birth of 70 and 96 tadpoles, respectively, from two females. Some of the tadpoles in one of these lots metamorphosed after 40 days in the laboratory, but some tadpoles in the other lot did not complete metamorphosis until 109 days. A newly hatched tadpole has a body length of 9.6 mm, and a total length of 25.2 mm; a recently metamorphosed young has a snout–vent length of 19.4 mm.

Tadpoles

A typical tadpole in Stage 37 (KU 170196) has a body length of 24.5 mm, and a total length of 59.3 mm. The body is ovoid in dorsal view, and is widest at about two-thirds the length of the body; the snout is a bluntly rounded. In lateral profile, the body is as deep as wide, and is highest posteriorly; the snout is round. The throat is convex. The eyes are moderately large, and are directed dorsolaterally. The interorbital distance is about 50% of the width of the body at the level of the orbits. The nostrils are midway between the eyes and the tip of the snout, and are directed anterolaterally. The spiracular tube is short and sinistral; the spiracular opening is transverse, and is directed posterodorsally on the ventrolateral surface at midlength of the body. The cloacal tube is median, short, and cone-shaped, with a transverse opening. The caudal musculature is moderately robust; its height is slightly more than that of the dorsal fin at midlength of the tail. The musculature terminates in a slender tip well within the margin of the caudal fins. The dorsal fin arises gradually from the posterior edge of the body. The dorsal and ventral fins are shallow, and are about equal in height at midlength of the tail; the fins terminate in an acute tip.

The width of the oral disc is equal to about one-third the width of the body. The disc is bordered laterally and ventrally by a single row of small blunt papillae. The two upper and three lower rows of labial teeth are about equal in length; the first lower row is narrowly interrupted medially. The upper jaw sheath is in the form of a continuous arch; the lower jaw sheath is massive, and is broadly V-shaped. Both sheaths bear weak blunt serrations.

In life the body is dull olive brown above, with greenish-tan flecks laterally. The belly is gray; the caudal musculature and fins are cream, with a dark brown dorsolateral line on the musculature. The iris is deep bronze.

Advertisement Call

The call consists of a loud "wraack," followed or not by a series of two to five notes, "tonk-tonk-tonk." No recordings are available.

Distribution and Ecology

This species is known from only a few localities, at elevations of 2000–2600 m in the cloud forest on the eastern slopes of the Cordillera Central in southcentral Colombia (Fig. 11.5). In March 1979, adults were found in dense bushes by day, and 1–2 m above the ground on more open bushes at night. Tadpoles were found in shallow grassy temporary pools.

Conservation Status

In the IUCN Red List, *Gastrotheca aureomaculata* is categorized as Near Threatened, both because of its small geographic range and because it is not known to exist in any protected areas.

Etymology

The specific epithet is derived from the Latin *aureus*, meaning "golden," and the Latin *maculatus*, meaning

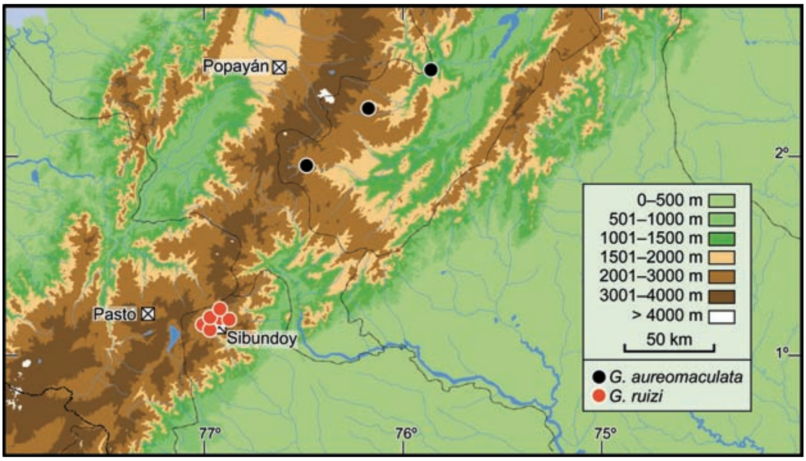

Fig. 11.5 Andean region of Colombia, showing the localities of known occurrences of *Gastrotheca aureomaculata* and *G. ruizi*.

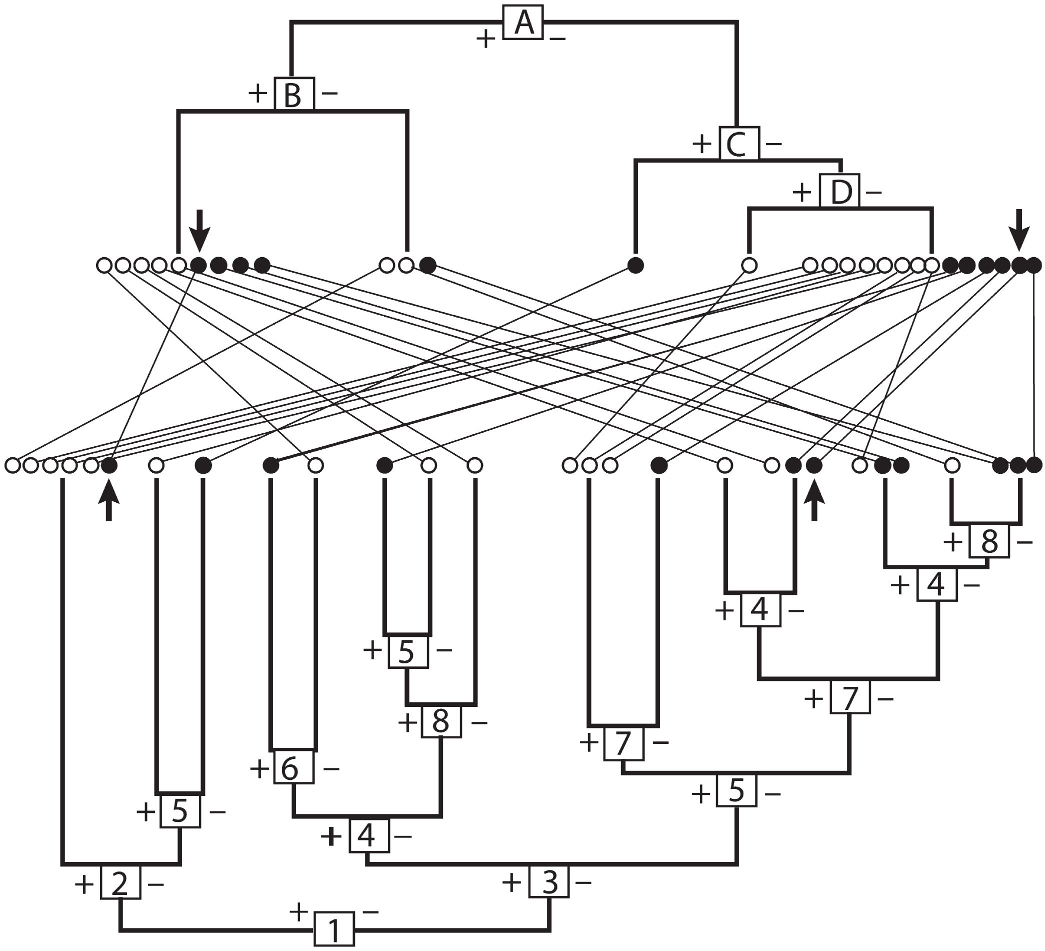

Fig. 11.6 Distance phenograms of the sums of squares of 28 adults of *Gastrotheca aureomaculata*. The upper phenogram is based on coded morphological characters: A = skin areolate; B = webbing on the fourth toe to a point midway between the antepenultimate and penultimate subarticular tubercles; C = webbing on the fifth toe to the distal subarticular tubercle; D = tubercle on the heel. The lower phenogram is based on coded coloration characters: 1 = dorsal surface of the shank patterned; 2 = dorsal pattern pale; 3 = anterior surface of the thigh patterned; 4 = venter patterned; 5 = dorsum patterned; 6 = venter pale; 7 = flank patterned; 8 = posterior surface of the thigh patterned. Characters are given in boxes at each dichotomy: + = character present; – = character absent. Open circles = males; solid circles = females. Symbols for the same individual in the two phenograms are connected by a line. The black arrows note the holotype of *G. aureomaculata*, and the gray arrows note the holotype of *G. mertensi*. All of the specimens in the major dichotomy to the left of 3 are spotted. Modified from Duellman (1983).

"spotted"; the name refers to the yellow-spotted dorsal surfaces of one of the color morphs of this species.

Remarks

All phylogenetic analyses place *Gastrotheca aureomaculata* as the sister species of *G. ruizi*. Both species have a biphasic life cycle.

Based on the specimens available at the time, Cochran and Goin (1970) recognized two distinctive species of *Gastrotheca*. More recent material from Moscapán, Colombia, includes specimens that are intermediate between the uniformly green frog named *G. mertensi* and the dark frog with pale spots named *G. aureomaculata*. Multivariate analyses of morphometric, structural, and color characters of 28 adults enabled Duellman (1983) to show that the named color patterns are extremes in a continuum of color variation (Fig. 11.6). The spotted pattern apparently develops ontogenetically. All of the metamorphosing young of a spotted female were uniformly green (Cochran and Goin, 1970).

Gastrotheca (*Duellmania*) *dunni* Lutz

Gastrotheca argenteovirens dunni Lutz, 1977.—Holotype: MNRJ 4092 from San Pedro, Departamento de Antioquia, Colombia.

Gastrotheca (*Duellmania*) *aureomaculata*—Dubois, 1987:33.

Gastrotheca dunni—Duellman, 1987:43.

Diagnosis

Adults of this medium-sized species attain a snout–vent length of 54.7 mm. The tibia length is less than 55% of the snout–vent length, and is about equal to the length of the foot. The interorbital distance is noticeably greater than the width of the upper eyelid. The skin on the dorsum is smooth, and is not co-ossified with the skull; transverse ridges are absent. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is shorter than the second. The discs are much wider than the digits. The fingers are unwebbed; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and a point midway between the penultimate and distal subarticular tubercles on the fifth toe. The dorsum is tan or green, usually with dark green or brown paravertebral marks. Markings on the head consist only of a pale labial stripe. A pale dorsolateral stripe usually is present. The flanks are gray, usually with dark spots; the venter is pale cream.

Gastrotheca dunni differs from *G. argenteovirens* and *G. trachyceps* in having proportionately shorter limbs and a narrower interorbital distance; it also lacks the blue flanks and black spots on the hidden surfaces of the thighs that are characteristic of those species. It lacks co-ossification of the skin with the underlying cranial elements, which is characteristic of *G. trachyceps*. It differs from other tadpole-producing species in the northern Andes in size and/or coloration. *G. aureomaculata* is much larger, and in life has a golden tympanum and a uniformly green dorsum and flanks, or is black or brown with pale spots on the dorsal surfaces. *G. espeletia* is about the same size as *G. dunni*, but differs by having the belly boldly marbled with black, and the first and second fingers equal in length. *G. ruizi* differs by having a long snout that is inclined anteroventrally.

Description

The following description is based on 55 specimens. The body is moderately robust; males attain a snout–vent length of 43.1 mm, and 54.7 mm in females. The head is slightly wider than long, and nearly as wide as the body. The snout is bluntly rounded in dorsal view and in profile. The canthus rostralis is weakly angular in cross-section. The loreal region is concave; the lips are slightly flared. The top of the head is flat. The interorbital distance is about 167% of the width of the upper eyelid. The internarial area is depressed. The nostrils are slightly protuberant, and are directed anterolaterally at a point below the anterior terminus of the canthus rostralis and at the level of the anterior margin of the lower jaw. The diameter of the eye is slightly greater than its distance from the nostril. The tympanum is nearly round, and is separated from the eye by a distance about half again the diameter of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately heavy and tubercular, obscures the upper edge of the tympanum, and curves posteroventrally from the posterior corner of orbit to a point above the insertion of the arm.

The arm is moderately robust, and lacks ulnar tubercles. The hand is moderate in size. The fingers are moderately long, and bear round discs; the width of the disc on the third finger is about 90% of the length of the tympanum. The relative lengths of the fingers are I < II < IV < III. The fingers are unwebbed. The subarticular tubercles are large and round; the supernumerary tubercles are large, and are present only on the proximal segments of the third and fourth fingers. The palmar tubercle is low and elongate; the prepollical tubercle is elongately elliptical, and is elevated; in males, the thumb bears a brown nuptial excrescence. The hind limb is robust. The tibia length and foot length are each about 46% of the snout–vent length. Calcars and tarsal tubercles are absent. An inner tarsal fold is present on the distal one-third of the tarsus. The outer metatarsal tubercle is diffuse or absent; the inner metatarsal tubercle is small, elliptical, elevated, and barely visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. The toes are about one-third webbed; the webbing formula is **I**(3^{-}–2)—(2–2^{+})**II**2—(3^{-}–3)**III**(2–2^{+})—3**IV**3–(1½–2) **V**. The subarticular tubercles are small and round; the supernumerary tubercles are low, diffuse, and present only on the proximal segments of the third, fourth, and fifth toes.

The skin on the dorsum is smooth; the skin on the flanks is weakly areolate; the skin on the belly and posteroventral surfaces of the thighs is granular; the other ventral surfaces are smooth. Cloacal tubercles and folds are absent. The pouch opening is V-shaped, with the anterior margin at the level of the posterior edge of the sacrum. The vocal sac is single, median, and subgular. The dentigerous processes of the vomers are nearly transverse, and are moderately separated medially at a level slightly posterior to the small round choanae. Each process bears five to seven teeth.

COLOR IN PRESERVATIVE

The dorsum is uniformly brown to dull gray (37%), or with dark brown paravertebral marks (34%) or dark flecks (29%). The flanks are uniformly gray (76%) or marked with dark spots (24%). A dark canthal stripe is absent. A pale dorsolateral stripe extends from the snout to midlength of the flank. A pale labial stripe is present, extending onto the flank in 95% of the individuals. A pale supracloacal stripe and a dark patch in the cloacal region are absent. The dorsal surfaces of the limbs are colored like the body, and have small dark flecks. The anterior and posterior surfaces of the thighs are uniformly brown. The venter is pale creamy gray, with black flecks in 17%. The vocal sac is gray.

COLOR IN LIFE

ICN 1153 from Yarumal, Departamento de Antioquia, Colombia.—The dorsum of the head and body were brown, with a pair of reddish-brown paravertebral marks beginning on the eyelids and extending to the cloacal region, and green spots lateral to the paravertebral marks (like what is shown in Fig. 11.7). The dorsolateral stripes were creamy buff; the stripes began on the snout, passed along the outer edge of the eyelid and the upper edge of the flank, and were confluent with the opposite member in the cloacal region. The labial stripe was creamy buff, and extended along the ventral edge of the flank. The loreal region was reddish brown. The tympanum was brown, with golden flecks. The dorsal surfaces of the limbs were brown, with green spots; the posterior surfaces of the thighs were uniformly gray. The venter was olive buff, with a blue infusion on the anterior part of the belly, and gray reticulations on the shanks. The iris was gold (translation of P. M. Ruíz-C. field notes, 28 April 1972).

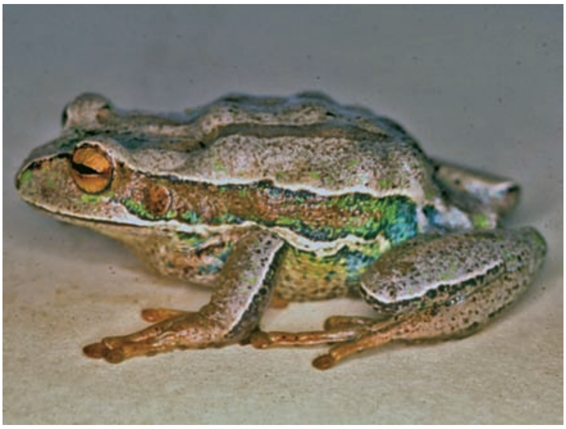

Fig. 11.7 *Gastrotheca dunni* (ICN 10055), female, 48.4 mm SVL, 3.5 km N Llanos de Cuiva, Antioquia, Colombia. Photo by J. D. Lynch, KUDA.

MEASUREMENTS

Females are slightly larger than males, but an ANOVA revealed that the differences are not significant (Table 11.4).

CRANIAL OSTEOLOGY

The dermal roofing bones are not co-ossified with the overlying skin; the sphenethmoid is sculptured. The nasals articulate medially; their borders are distinct from the sphenethmoid. The frontoparietals have an incomplete articulation medially; each bears a moderate supraorbital flange, and an otic flange that does not articulate with the squamosal. A temporal arcade is absent. The carotid canal is enclosed. The preorbital process is separated from the facial process of the maxilla by a notch; a postorbital process is present. The head of the squamosal has a narrow crest; the zygomatic ramus extends to the maxilla. The otic ramus of the squamosal completely articulates with and moderately overlaps the ossified crista parotica; an auxiliary dorsal ramus is present. The parasphenoid has a short posteromedian process; the cultriform process terminates posterior to the level of the neopalatines. The paraspenoid alae articulate with the pterygoids. The neopalatines are moderately separated medially, form the posterior margins of the choanae, and have a serrate ventral ridge. The pterygoid articulates with the squamosal; the median ramus of the pterygoid is not expanded medially; an auxiliary dorsal ramus is present.

Life History

One female (MLS) from San Pedro contained 46 eggs, each 6 mm in diameter, in the pouch. This corresponds to the number and size of eggs brooded by *Gastrotheca argenteovirens*, in which the eggs hatch into aquatic lar-

Table 11.4 Univariate statistics for adults of *Gastrotheca dunni*

	Males (n = 15)			Females (n = 40)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	37.8	32.0–43.1	2.90	44.8	32.7–54.7	5.32
Tibia length	17.2	13.4–19.0	1.58	20.6	15.0–24.2	2.58
Foot length	17.5	15.3–19.4	0.34	20.9	13.9–25.1	3.00
Head length	12.9	11.2–14.1	0.91	15.1	11.9–17.3	1.44
Head width	14.1	11.9–16.0	1.04	16.2	11.3–18.5	1.90
Interorbital distance	4.1	3.7–4.5	0.23	5.0	3.7–6.0	0.65
Eyelid width	2.8	2.0–3.3	0.42	3.0	2.1–3.8	0.39
Internarial distance	2.4	1.9–2.9	0.26	2.8	1.8–3.6	0.39
Eye diameter	3.9	3.3–4.6	0.34	4.4	4.3–5.2	0.51
Eye–nostril distance	3.6	3.0–4.0	0.22	4.1	3.3–4.8	0.36
Orbit–jaw distance	1.9	1.5–2.3	0.22	2.4	1.4–3.0	0.39
Nostril–jaw distance	2.6	2.2–3.0	0.23	3.3	1.9–4.4	0.52
Tympanum diameter	2.0	1.5–2.3	0.18	2.4	1.6–3.0	0.34
Thumb length	6.7	5.4–7.6	0.59	7.9	5.6–9.5	1.05
Third finger length	12.8	10.8–14.6	1.02	15.0	10.5–18.0	1.96
Disc width	1.8	1.6–2.0	0.14	2.2	1.3–2.6	0.28

vae in Stages 34–37. Thus it is assumed that *G. dunni* produces advanced tadpoles.

Advertisement Call

The call consists of a long guttural note, usually followed by a series of short notes.

Distribution and Ecology

This species occurs in cultivated lands and remnants of cloud forest at elevations of 2000–2700 m north of Río Medellín in the northern part of the Cordillera Central of the Andes, in Departamento de Antioquia, Colombia (Fig. 11.2). At night the frogs perch on bushes and low trees.

Conservation Status

In the IUCN Red List, this species is categorized as being of Least Concern because it is common, but it is not known from any protected areas.

Etymology

The specific name *dunni* is a patronym for Emmett R. Dunn, in recognition of his contributions to our knowledge of amphibians and reptiles in Colombia.

Remarks

This taxon was first recognized as a subspecies of *Gastrotheca argenteovirens* (Lutz, 1977). A multivariate analysis of morphometric and structural data revealed that *G. dunni* exhibits consistent differences in size and extent of the webbing from *G. argenteovirens*, as well as differences in coloration (Duellman, 1987).

Gastrotheca (*Duellmania*) *dysprosita* Duellman

Gastrotheca dysprosita Duellman, 2013:4.—Holotype: KU 212078 from Abra Barro Negro, 27 km [by road] WSW Leimebamba, Región de Amazonas, Peru.

Diagnosis

Males attain a maximum known snout–vent length of 60.5 mm; females are unknown. The tibia length is less than 50% of the snout–vent length, and is longer than the foot. The interorbital distance is less than the width of the upper eyelid. The skin on the dorsum is granular, not co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is granular. The first and second fingers are equal in length. The discs on the fingers are slightly wider than the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends to the antepenultimate subarticular tubercle on Toe IV and the penultimate subarticular tubercle on Toe V. The dorsum is green, with a narrow irregularly margined yellow middorsal stripe and a similar dorsolateral stripe. The flanks are green, with small yellow spots. The venter is cream, with small brown spots.

Gastrotheca dysprosita differs from other members of the subgenera *Duellmania* and *Gastrotheca* by having a green dorsum with a yellow middorsal stripe, and green flanks with small yellow spots. Furthermore, *G. dysprosita* lacks a dark canthal stripe and pale labial stripe, features that are present in most individuals of the other species. *G. dysprosita* is like *G. monticola* in having a bluntly rounded snout in profile, whereas the snout is truncate in *G. lateonota*, and inclined anteroventrally in *G. stictopleura*. In *G. dysprosita* and *G. monticola*, the frontoparietals broadly contact the median flanges of the squamosals to form a temporal arcade. In *G. lateonota* and *G. stictopleura*, the frontoparietals do not extend laterally to articulate with the squamosals.

Description

The following description is based on two males having respective snout–vent lengths of 45.9 and 60.5 mm. The body is moderately robust. The head is slightly wider than long, and as wide as the body. The snout is bluntly rounded in dorsal view and in profile. The canthus rostralis is slightly curved, and is round in cross-section. The loreal region is barely concave; the lips are rounded. The top of the head is flat. The interorbital distance is 92% of the width of the upper eyelid. The internarial area is depressed. The nostrils are not protuberant, and are directed laterally below the anterior terminus of canthus rostralis at a level slightly posterior to the anterior margin of the lower jaw. The diameter of the eye is much greater than its distance from the nostril. The tympanum is round, and is separated from the eye by a distance about two-thirds the length of tympanum. The tympanic annulus is barely distinct, and is coarsely granular. The supratympanic fold is moderately weak, extends from the posterior corner of the orbit to a point above the angle of the jaw, and barely obscures the upper edge of the tympanum.

The arm is moderately slender, and lacks ulnar tubercles. The hand is moderate in size. The fingers are long and unwebbed. The discs on the fingers are rather small; the digit adjacent to the disc is 60% of the width of the disc on the third finger; the width of the disc on the third finger is 66% of the length of the tympanum. The relative lengths of the fingers are I = II < IV < III. The subarticular tubercles are low and rounded; none are bifid. The supernumerary tubercles are small, subconical, and numerous on the proximal segments. The palmar tubercle is low and bifid; the prepollical tubercle is low and elliptical; nuptial excrescences are absent. The hind limb is rather short and moderately slender. The tibia length is 46.4% of the snout–vent length; the foot length is 40.2% of the snout–vent length. The heel lacks a calcar or tubercle; an outer tarsal fold is absent. The inner tarsal fold is distinct on the distal one-fifth of the tarsus. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is small, elliptical, and not visible from above. The toes are moderately long and slender. The relative lengths of the toes are I < II < III < V < IV. The outer toes are about one-fourth webbed; the webbing formula is **III**1½–3**IV**3–2**V**. The subarticular tubercles are low and round; the supernumerary tubercles are small, round, and numerous on the proximal segments.

The skin on all surfaces is coarsely granular; cloacal folds and tubercles are absent. The dentigerous processes of the vomers are inclined posteromedially, and are widely separated medially between the large round choanae. Each process bears seven teeth. The tongue is cordiform, shallowly notched posteriorly, and free behind for about one-third of its length. The vocal slits are short, and diagonal between the base of the tongue and the angle of the jaw.

COLOR IN PRESERVATIVE

The dorsum, the flanks, and the head are dark brown. The digits are colored like the dorsum, except that Fingers I and II are cream, with small brown spots. A narrow irregularly margined cream middorsal stripe extends from the posterior margin of the head to a point slightly posterior to the sacrum. A similar cream dorsolateral stripe extends from a point above the tympanum to the groin. The flanks and the anterior and posterior surfaces of the thighs are brown, with small irregularly shaped cream spots. An interorbital bar and canthal and labial stripes or bars are absent. The venter is cream, with small brown spots on the chest and laterally on the belly. The vocal sac is brown.

COLOR IN LIFE

The dorsum of KU 212078 was bright green, with middorsal and dorsolateral irregular bronzy-cream stripes. The flanks were green, with cream and black spots (Fig. 11.8). The anterior and posterior surfaces of the thighs were mottled cream and black. The throat was dark green; the vocal sac was dull brown medially. The belly was cream, with black flecks. The iris was reddish copper.

MEASUREMENTS

The respective measurements of two males (KU 212078 and UF 30080) are as follows: snout–vent length 60.5, 45.9; tibia length 28.1, 23.4; foot length 24.3, 22.5; head length 20.0, 18.5; head width 21.7, 17.7; interorbital distance 6.0, 4.9; upper eyelid width 5.6, 5.2; internarial

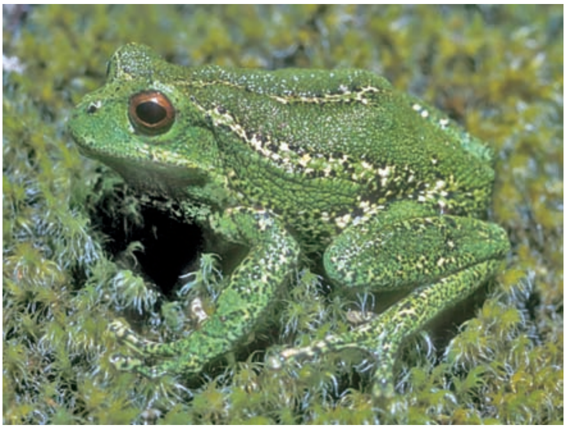

Fig. 11.8 *Gastrotheca dysprosita* (KU 212078), male, 60.5 mm SVL, Abra Barro Negro, 3440 m, Amazonas, Peru. Photo by W. E. Duellman.

distance 3.8, 4.1; eye diameter 6.2, 5.6; eye–nostril distance 3.8, 3.5; orbit–jaw distance 3.3, 2.6; nostril–jaw distance 4.5, 4.0; tympanum diameter 3.8, 3.6; thumb length 11.2, 10.2; third finger length 18.8, 16.2; and width of disc on third finger 2.5, 2.3.

CRANIAL OSTEOLOGY

A temporal arcade exists, the only osteological feature could be determined by a probe.

Life History

Because this species is known only from two males, there is no direct evidence on reproduction. Duellman (2013) suggested that the species probably developed eggs that hatched as tadpoles, a mode that is characteristic of its presumed closest relatives.

Advertisement Call

At the type locality, calls presumably of this species were heard by day and night during rains in January and in March. The presumed call consists of three or four short notes.

Distribution and Ecology

Gastrotheca dysprosita is known only from elevations of 3320–3440 m in the vicinity of the type locality, in the northwestern part of the Cordillera Central in northern Peru (Fig. 11.9). The holotype was sitting on a mossy cliff during rain by day. On Abra Barro Negro, there is a mixture of elfin forest containing moss, lichens, and some bromeliads at elevations of up to about 3350 meters, above which is puna, consisting of moss, lichens, and a bunchgrass (*Stipa*).

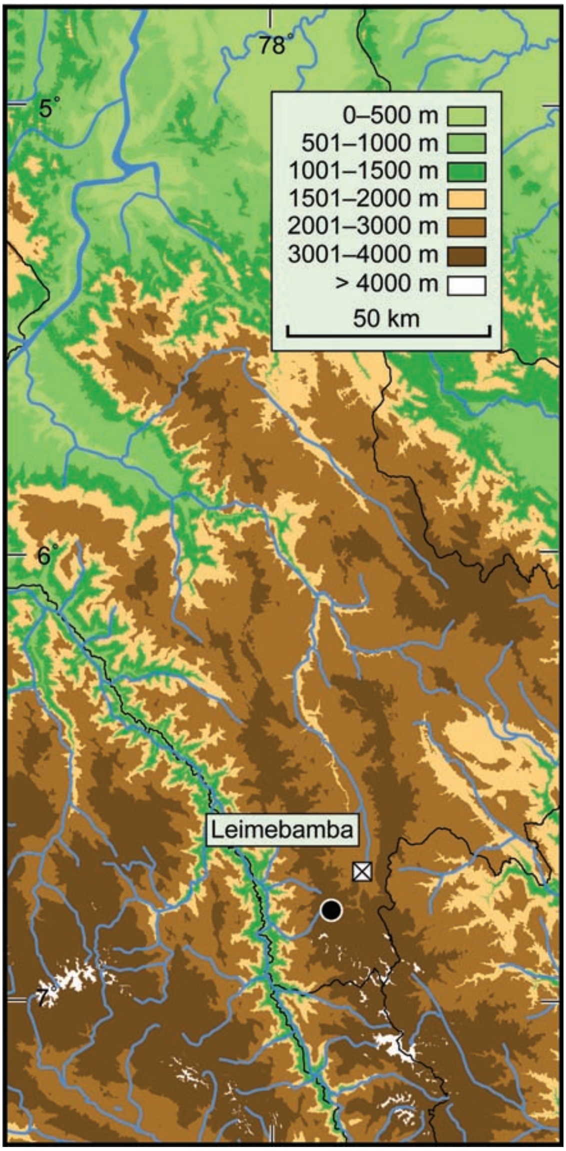

Fig. 11.9 Andean region of northern Peru, showing the locality of known occurrences of *Gastrotheca dysprosita*.

Conservation Status

The data are insufficient to categorize this species.

Etymology

According to the original description, the specific name is derived from the Greek adjective *dysprositos*, meaning "hard to get at." The name was used in reference to the difficulty in finding this elusive frog.

Remarks

As noted by Duellman (2013), the tissue taken from the holotype for genomic analysis was degraded, so no DNA could be extracted. Consequently, the genetic relationships of this species are unknown. Instead of being a relative of *Gastrotheca monticola*, as treated here, it might be a relative of *G. aguaruna* and thus be a member of the subgenus *Gastrotheca*.

Gastrotheca (*Duellmania*) *espeletia* Duellman and Hillis

Gastrotheca espeletia Duellman and Hillis, 1987:146.—Holotype: KU 169401 from N shore Lago de la Cocha, 2790 m, Departamento de Nariño, Colombia.

Diagnosis

Adults of this medium-sized species attain a snout–vent length of 52.6 mm. The tibia length is less than 50% of the snout–vent length, and is slightly shorter than the length of the foot. The interorbital distance is about equal to the width of the upper eyelid. The skin on the dorsum is smooth, and is not co-ossified with the skull; transverse ridges are absent. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is longer than the second. The discs are barely wider than the digits. The fingers are unwebbed; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and a point midway between the penultimate and distal subarticular tubercles on the fifth toe. The dorsum is gray, green, or tan, with darker paravertebral marks. Markings on the head usually consist of a pale labial stripe and dark canthal stripe. A pale dorsolateral stripe is absent. The flanks are gray, usually with dark spots; the venter is dull cream, with black mottling.

Gastrotheca espeletia is like *G. pseustes* and *G. riobambae* in having short limbs and small digital discs. It differs from *G. pseustes* in having bold spots or mottling (or being uniformly dark gray) ventrally, as contrasted to diffuse gray spots or a pale venter in *G. pseustes*; furthermore, the snout is narrower in *G. espeletia* than in *G. pseustes*. In *G. pseustes* and *G. riobambae*, the first and second fingers are equal in length, whereas the first finger is longer than the second in *G. espeletia*; the webbing on the feet is more extensive in *G. riobambae*. Tadpoles of *G. espeletia* differ from those of *G. pseustes* and *G. riobambae* and are like those of *G. psychrophila* in having the dorsal fin arise abruptly from the body. In addition, the marginal papillae are in a single row ventromedially and in two alternating rows ventrolaterally in *G. espeletia*, whereas they are in two alternating rows along the entire ventral lip in the others.

Description

The following description is based on 40 specimens. The body is robust; males attain a snout–vent length of 52.6 mm, and 51.9 mm in females. The head is slightly wider than long, and about as wide as the body. The snout is acutely rounded in dorsal view, and is rounded in lateral profile, protruding well beyond the margin of the jaws. The canthus rostralis is angular in cross-section. The loreal region is slightly concave; the lips are rounded. The top of the head is concave. The interorbital distance is slightly greater than the width of the upper eyelid. The internarial area is slightly depressed. The nostrils are slightly protuberant, and are directed dorsolaterally at a point just behind the anterior margin of the lower jaw and below the anterior terminus of the canthus rostralis. The diameter of the eye is slightly less than its distance from the nostril. The tympanum is vertically ovoid, and is separated from the eye by a distance 1.5 times the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is weak, and extends from the posterior corner of the eye to a point above the insertion of the arm.

The arm is robust. The hand is moderate in size. The fingers are unwebbed. The discs on the fingers are small, round, and barely wider than the digits; the width of the disc on the third finger is about 60% of the length of the tympanum. The relative lengths of the fingers are I > II < IV < III. The subarticular tubercles are small, subconical, and not bifid; supernumerary tubercles are few, minute, and present only on the proximal segments of the fingers. The palmar tubercle is bifid; the prepollical tubercle is elongately ovoid; in males, the thumb bears brown nuptial excrescences medially. The hind limb is moderately short and robust. The tibia length is about 38% of the snout–vent length; the foot length is about 43% of the snout–vent length. A calcar is absent on the heel; tarsal folds are absent. The outer metatarsal tubercle is minute; the inner metatarsal tubercle is ovoid, and is not visible from above. The toes are long. The relative lengths of the toes are I < II < III = V < IV. The toes are about one-third webbed; the webbing formula is **I**2—2^{+}**II**3^{-}—3**III**2—3**IV**3—2^{-}**V**. The subarticular tubercles are small; the supernumerary tubercles are minute, and are present only on the proximal segments of the toes.

The skin on the dorsum of the head, body, and limbs is smooth; eyelid tubercles are absent. The skin on the flanks is areolate; the skin on the belly and the ventral surfaces of the thighs is granular. Cloacal folds and tubercles are absent. The pouch opening is narrowly V-shaped, with the anterior border at the level of the sacrum. The dentigerous processes of the vomers are inclined posteromedially, and are separated medially between the posterior margins of the small ovoid choanae. Each process bears four to six teeth.

COLOR IN PRESERVATIVE

The dorsum is dull gray to tan, with darker longitudinal paravertebral markings on the body, and (usually) dark spots on the shanks. The flanks are gray or tan, with dark spots in 78% of the specimens. The anterior and posterior surfaces of the thighs are pale gray, with black spots or mottling. The ventral surfaces of the body and shanks are either dull cream with heavy black mottling or flecks, or these surfaces are dark gray; the vocal sac also is dark gray. Pale dorsolateral and supracloacal stripes are absent in all specimens; pale labial stripes are absent in 78%. A dark canthal stripe usually (78%) is present.

COLOR IN LIFE

The coloration is highly variable, ranging from dull dark brown to tan with brown markings, or to green with dark green markings (Fig. 11.10).

KU 169401–2 from Lago de la Cocha, Departamento de Nariño, Colombia.—The dorsum was metallic bronze brown, with pale green flecks dorsolaterally. The axilla, groin, anterior and posterior surfaces of the thighs, and inner surfaces of the shanks were greenish blue. The vocal sac was gray; the rest of the venter was dull bluish gray. The iris was reddish brown, with fine black reticulations (W. E. Duellman field notes, 24 September 1974).

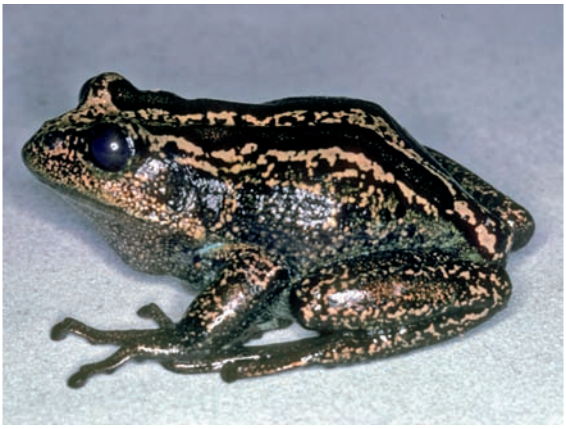

Fig. 11.10 *Gastrotheca espeletia* (KU 169401, holotype), male, 52.6 SVL, Lago de la Cocha, Nariño, Colombia. Photo by W. E. Duellman.

KU 117979 from Tulcán, Provincia de Carchi, Ecuador.—The dorsum was pale brown, with dark brown markings edged in white. There was a green wash above the tympanum, in the axilla, and in the groin. The flanks and posterior surfaces of the thighs were washed with blue green and spotted with brown. The venter was pale dirty yellow, flecked with gray. The iris was a rich chocolate brown (J. D. Lynch field notes, 23 February 1968).

KU 178558 from El Carmelo, Provincia de Carchi, Ecuador.—The dorsum was pea green, with darker green markings edged with black or cream. The upper flanks were darker green; the lower flanks were pale yellow. The venter was creamy white; the groin and hidden surfaces of the thighs were pale blue. A postocular blotch was brown, with some orange; the iris was coppery brown (J. D. Lynch field notes, 22 July 1977).

MEASUREMENTS

From the small number of available adults, males and females seem to be about the same size (Table 11.5).

CRANIAL OSTEOLOGY

The sphenethmoid is smooth and unsculptured; the other bones of the skull table bear a coarse pit-and-ridge dermal sculpturing; thus the skull table has a heterogeneous pattern. The nasals articulate medially, and are fused to one another and the sphenethmoid posteriorly; posterolaterally, the nasals articulate at the anterolateral margin of the frontoparietals. The frontoparietals have a complete articulation medially; they lack an evident supraorbital flange, but a small otic flange is present. A temporal arcade is absent. The frontoparietal covers only the anterior epiotic eminence; the carotid canal is open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae bear long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for about half the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is short. The postorbital process of the maxilla is massive, and has a broad horizontal articulation with the wide zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the narrow otic plate articulates marginally with the crista parotica. The dor-

Table 11.5 Univariate statistics for adults of *Gastrotheca espeletia*

	Males ($n = 3$)			Females ($n = 6$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	49.4	47.0–52.6	2.87	47.5	44.3–51.9	3.50
Tibia length	19.5	16.6–21.4	2.55	17.5	16.7–19.8	1.18
Foot length	22.1	18.8–24.1	2.86	20.2	18.7–23.0	1.70
Head length	16.2	15.2–17.4	1.11	15.9	14.9–17.3	0.93
Head width	17.8	16.4–19.2	1.40	17.7	16.5–19.3	1.07
Interorbital distance	4.3	3.6–4.9	0.65	3.9	3.6–4.3	0.28
Eyelid width	3.7	3.5–4.1	0.32	3.6	3.2–4.2	0.36
Internarial distance	2.8	2.5–3.0	0.27	2.9	2.6–3.2	0.21
Eye diameter	4.5	4.4–4.6	0.12	4.1	3.7–4.5	0.28
Eye–nostril distance	3.5	3.2–4.0	0.44	3.5	3.2–3.8	0.25
Orbit–jaw distance	2.8	2.7–3.1	0.23	2.7	2.3–3.1	0.32
Nostril–jaw distance	3.6	3.3–3.9	0.31	3.4	2.8–4.1	0.42
Tympanum diameter	2.2	1.8–2.5	0.36	2.5	2.2–2.7	0.19
Thumb length	9.5	8.1–10.3	1.22	8.9	7.5–10.4	1.02
Third finger length	16.0	13.2–18.0	2.48	14.8	13.4–16.3	1.20
Disc width	1.9	1.7–2.1	0.21	1.9	1.6–2.3	0.27

sal part of the stapedial footplate is two to three times the length of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified posterior to the midlength of the orbit, but is not synostosed with the prootic. The neopalatines are moderately separated medially; each bears a ventral flange. The pterygoid articulates with the medial surfaces of the zygomatic ramus of the squamosal and the postorbital process of the maxilla via a long acuminate recurved process on the anterior ramus of the pterygoid. The vomers bear small dentigerous processes located between the middle quadrants of the choanae.

Life History

Males have been found calling both by day and night from bunchgrass. Most tadpoles have been found in grassy ponds in páramo, but some were in a pond in a pasture, and others were in drainage ditches. Tadpoles in nearly all stages of development have been found in February, May, and July; recently metamorphosed young were found in July. *G. espeletia* presumably has a long, if not continuous, breeding season in the wet páramos, and tadpoles may require many months to develop.

Tadpoles

A typical tadpole in Stage 35 (KU 203541) has a body length of 25 mm, and a total length of 67 mm. In dorsal view the body is ovoid, narrowed anteriorly, and widest at three-fourths the length of the body; the snout is bluntly rounded. In lateral profile, the body is highest at three-fourths the length of the body, but is not as high as wide; the snout is inclined from the nostrils to a truncate tip. The throat is convex. The eyes are small, and are directed dorsolaterally. The interorbital distance is more than 33% of the width of the body at the level of the orbits. The nostrils are midway between the eyes and the tip of the snout, and are directed anterolaterally. The spiracular tube is short and sinistral, with a U-shaped opening directed posterodorsally on the ventrolateral surface at midlength of the body. The cloacal tube is short, conical, and median, with a transverse opening. The caudal musculature is moderately robust; its height is slightly less than that of the dorsal fin at midlength of the tail. The musculature terminates gradually in a pointed tip well within the margin of the caudal fin. The dorsal fin arises abruptly from the posterior edge of body; the dorsal and ventral fins are equal in height, and terminate in an acutely rounded tip.

The width of the oral disc is equal to about half the width of the body. The disc is bordered laterally and ventrolaterally by two alternating rows of marginal papillae, and ventromedially by a single row of blunt papillae. There are two upper and three lower rows of labial teeth; the rows are about equal in length; the first lower row is narrowly interrupted medially. The upper jaw sheath is massive, and forms a continuous broad arch; the lower jaw sheath is broadly V-shaped; the sheaths have barely noticeable serrations.

In preservative the dorsum of the body and the caudal musculature are dull grayish brown. The belly is dull bluish gray. The lateral and ventral surfaces of the caudal musculature are tan; the caudal fins have minute brown flecks. In life the body is grayish green, with yellow flecks on the tail.

Advertisement Call.

The call consists of two or three short cluck-like notes; the pulsed notes have a dominant frequency of ± 1260 Hz (Sinsch and Juraske, 2006).

Distribution and Ecology

Gastrotheca espeletia occurs at elevations of 2530–3400 m in the southern part of the Cordillera Central in Colombia and in the Nudo de Pasto in southern Colombia and northern Ecuador (Fig. 11.11). A record for Ricuarte (ANSP 25316) at an elevation of 1180 m on the Pacific slopes of the Cordillera Occidental in southern Colombia is thought to be erroneous. The southern end of the range in the western cordillera in Ecuador seems to be limited by the dry valley of the Río Chonta. In the Cordillera Oriental in Ecuador, the range may abut or overlap that of *G. riobambae*, but no specimens are available from the critical area. *G. espeletia* occurs on the high Amazonian slopes of the Cordillera Oriental at elevations of 2650–2710 m in the upper valley of the Río Chingual; there it occurs sympatrically with the larger *G. orophylax*. At night, individuals of *G. orophylax* commonly are perched on the huge leaves of *Gunnera* (Haloragaceae), whereas *G. espeletia* are on the ground or on low (< 50 cm) herbs. The range of *G. espeletia* overlaps that of *G. argenteovirens* in the vicinity of Pasto in southern Colombia; both species have been recorded from Pasto, but they have not been found in microsympatry.

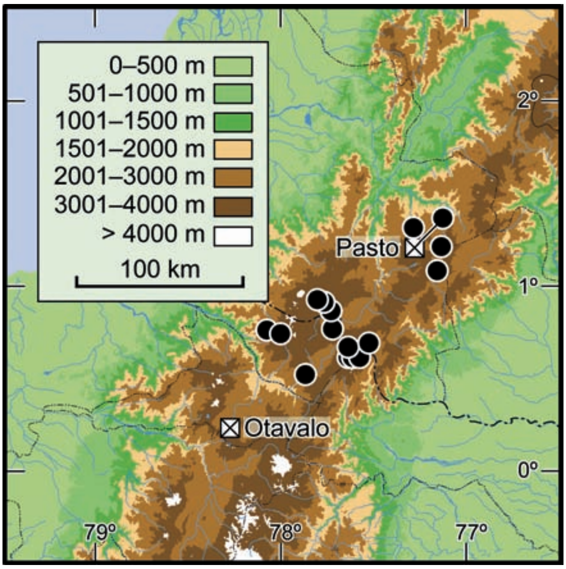

Fig. 11.11 Andean region of southern Colombia and northern Peru, showing the localities of known occurrences of *Gastrotheca espeletia*.

Although *Gastrotheca espeletia* descends to subpáramo and cultivated areas, it seems to be associated primarily with páramos characterized by *Espeletia pycnophylla* (Asteraceae). With the exception of an outlying area in the Cordillera de los Llanganati in central Ecuador, *Espeletia* reaches its southernmost distribution in the Páramo de Angel in northern Ecuador (Cuatrecasas, 1979), which also is the southern terminus of the range of *G. espeletia*.

Conservation Status

Gastrotheca espeletia is listed as Endangered in the IUCN Red List, both because of destructive agricultural practices in its small area of known distribution, and because the species is not known to occur in any protected areas.

Etymology

The specific name *espeletia* is a noun in apposition, referring to the genus *Espeletia*, a characteristic plant in the páramos inhabited by this species (Duellman and Hillis, 1987).

Remarks

Morphometrically, this species falls within the range of *Gastrotheca riobambae*, from which *G. espeletia* was distinguished allozymically by Duellman and Hillis (1987).

Gastrotheca (*Duellmania*) *litonedis* Duellman and Hillis

Gastrotheca litonedis Duellman and Hillis, 1987:149.—Holotype: KU 202690 from 10 km [by road] NW Girón, Provincia de Azuay, Ecuador, 2750 m.

Diagnosis

Adults of this medium-sized species attain a snout–vent length of 62.4 mm. The tibia length is less than 50% of the snout–vent length, and is about as long as the foot. The interorbital distance is about twice the width of the upper eyelid. The skin on the dorsum is smooth, areolate, or granular; it lacks transverse ridges and co-ossification with the bones of the skull. Supraciliary processes are absent. The heels lack calcars and tubercles. The tympanic annulus is smooth. The first and second fingers are equal in length. The discs on the fingers are slightly wider than the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is tan or green, with or without darker paravertebral marks. Markings on the head consist of a pale labial stripe. A pale dorsolateral stripe usually is present. The flanks are brown, with or without dark brown spots; the venter is uniformly pale cream.

Gastrotheca litonedis is sympatric with *G. lojana* and *G. pseustes*, from which it differs by having finely granular skin on the dorsum, as opposed to coarsely granular skin in those species; both of which further differ from *G. litonedis* by having cream venters with dark spots, instead of a uniformly pale venter. *G. litonedis* differs from *G. espeletia* and *G. riobambae* by lacking ventral markings, and from *G. argenteovirens*, *dunni*, and *monticola* by lacking black and blue mottling on the hidden surfaces of the thighs. It also differs from all of these species by having a proportionately wider interorbital distance. *G. lateonota* is like *G. litonedis* in lacking spots on the venter, which is brownish gray in *G. lateonota*, as opposed to cream in *G. litonedis*; furthermore, in profile the snout is truncate in *G. lateonota* and rounded in *G. litonedis*.

Description

The following description is based on 24 specimens. The body is moderately robust. The maximum snout–vent length is 52.5 mm in males, and 62.4 mm in females. The head is slightly wider than long, and as wide as the body. The snout is rounded in dorsal view, and is bluntly rounded in profile. The canthus rostralis is angular in cross-section. The loreal region is barely concave; the lips are rounded. The top of the head is slightly concave. The interorbital distance is about twice the width of the upper eyelid. The internarial area is flat. The nostrils are barely protuberant, and are directed laterally at the level of the anterior margin of the lower lip and at the terminus of the canthus rostralis. The diameter of the eye is slightly less than its distance from the nostril. The tympanum is vertically ovoid, and is separated from the eye by a distance slightly greater than the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately thick, and extends from the posterior corner of eye to a point above the insertion of the forearm.

The arm is moderately robust, and lacks ulnar tubercles. The hand is moderate in size. The fingers are unwebbed. The discs on the fingers are small and round; the width of the disc on the third finger is equal to the length of the tympanum. The relative lengths of the fingers are I = II < IV < III. The subarticular tubercles are moderately large and round. The supernumerary tubercles are small and few in number, occurring only on the proximal segments. The palmar tubercle is not bifid; the prepollical tubercle is elongate and ovoid; a patch of brown nuptial excrescences is present on the medial base of the thumb. The hind limb is moderately short and robust. The tibia length is about 44% of the snout–vent length; the foot length is about 45% of the snout–vent length. The heels lack calcars and tubercles. An outer tarsal fold is absent; a weak inner tarsal fold is present on the distal half of the tarsus. The inner metatarsal tubercle is large, flat, ovoid, and not visible from above; an outer metatarsal tubercle is absent. The toes are long. The relative lengths of the toes are I < II < III = V < IV. The toes are about one-third webbed, with no web between the first and second toes; the webbing formula for the other toes is **II**1½–3**III**2–3^{+}**IV**3–2^{-}**V**. The subarticular tubercles are moderately small and round; the supernumerary tubercles are small, and present only on the proximal segments.

The texture of the skin on the dorsum of the head, body, and limbs is variable: areolate (50%), smooth (21%), granular (21%), or pustular (8%). The skin on the flanks is smooth; the skin on the belly and ventral surfaces of the thighs is granular. Tubercles are absent on the upper eyelids. Cloacal folds and tubercles are absent. The opening of the brood pouch is U-shaped, with the anterior border at the level of the sacrum. The dentigerous processes of the vomers are slightly inclined posteromedially, and are narrowly separated medially between the small round choanae. Each process bears five to seven teeth.

COLOR IN PRESERVATIVE

The dorsum is either uniformly tan to bluish gray (38%) or has dark brown or green markings, usually (54%) in the form of longitudinal paravertebral marks. The flanks are uniformly pale brown (68%), or have dark (25%) or pale (7%) spots. The dorsal surfaces of shanks are uniform (46%), or marked with dark spots (42%) or bars (12%). The anterior and posterior surfaces of the thighs usually (96%) are uniformly tan or gray, but some (4%) have dark spots. The ventral surfaces of the body and the limbs are uniformly pale cream (96%) or have small black flecks (4%). A dark canthal stripe usually (96%) is absent; a pale labial stripe usually (96%) is present. A pale dorsolateral stripe usually (79%) is present; a pale supracloacal stripe is absent.

COLOR IN LIFE

Some individuals, such as the holotype, have a uniformly green dorsum (Fig. 11.12A), whereas others have a tan dorsum. Dark brown dorsal markings are present in some individuals (Fig. 11.12B). The flanks are bronze brown. The axilla, groin, and hidden surfaces of the limbs are pale blue; the venter is creamy gray. The iris is deep bronze, with black reticulations.

MEASUREMENTS

In all but two measurements, the means of females are significantly larger than those of males (Table 11.6).

CRANIAL OSTEOLOGY

No skeletal preparations are available.

Life History

Gastrotheca litonedis broods eggs that hatch as tadpoles (S. Carvajal-Endara, pers. comm.).

Advertisement Call

The call is one that is typical of the high Andean species of *Gastrotheca*: a single note, “wronk,” followed or not by two or three shorter notes, “tonk-tonk.”

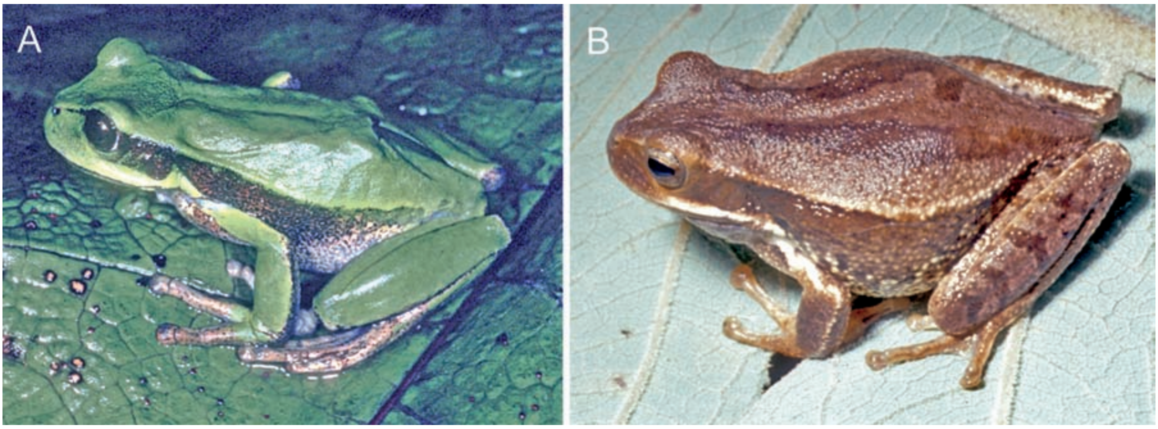

Fig. 11.12 *Gastrotheca litonedis*. A: KU 202690 (holotype), female, 62.4 mm SVL, 10 km NW Girón, Azuay, Ecuador. B: QCAZ 2692, male, 56.4 mm SVL, Oña, Azuay, Ecuador. Photos by W. E. Duellman (A) and L. A. Coloma (B), KUDA.

Table 11.6 Univariate statistics for adults of *Gastrotheca litonedis*

	Males (n = 13)			Females (n = 22)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length**	53.8	48.9–57.4	2.77	58.0	53.5–62.4	2.44
Tibia length**	25.9	23.5–27.4	1.13	28.7	23.3–31.6	1.91
Foot length**	24.6	17.9–27.2	2.40	27.7	19.0–30.4	2.41
Head length**	17.6	16.5–19.0	0.64	19.2	18.1–20.5	0.72
Head width**	19.0	17.6–20.1	0.79	20.5	18.7–22.2	0.92
Interorbital distance**	6.8	6.2–7.6	0.42	7.7	7.0–8.5	0.42
Eyelid width	4.6	3.8–5.2	0.36	4.8	4.2–5.7	0.37
Internarial distance**	3.2	2.6–3.7	0.30	3.5	3.0–4.2	0.30
Eye diameter**	5.1	4.5–5.5	0.37	5.4	4.8–5.9	0.31
Eye–nostril distance**	4.9	4.7–5.4	0.16	5.5	4.9–6.2	0.29
Orbit–jaw distance*	2.7	2.3–4.6	0.64	3.1	2.4–3.6	0.30
Nostril–jaw distance	4.0	3.4–4.6	0.30	4.1	3.6–4.6	0.27
Tympanum diameter**	3.5	2.9–4.0	0.31	3.8	3.2–4.3	0.26
Thumb length**	10.1	9.2–11.0	0.65	10.9	8.9–12.2	0.85
Third finger length**	17.1	16.0–18.1	0.66	19.3	17.4–21.5	1.07
Disc width*	3.1	2.5–3.5	0.34	3.4	2.7–4.1	0.38

*Differences between the means of the sexes are significant (ANOVA, $P \leq 0.05$).

**Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

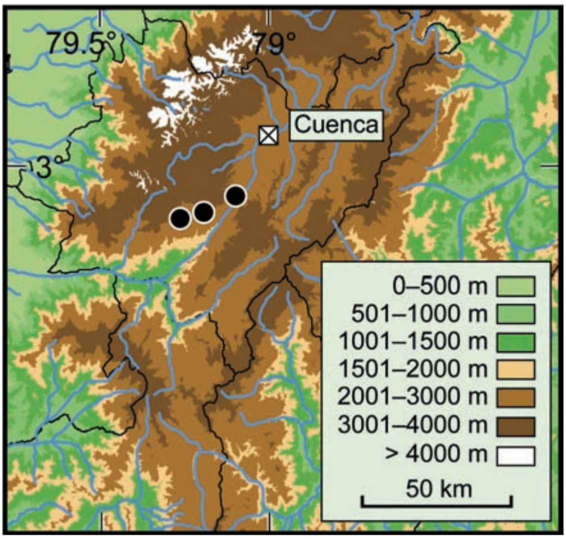

Fig. 11.13 Andean region of southern Ecuador, showing the localities of known occurrences of *Gastrotheca litonedis*.

Distribution and Ecology

This species is known only from three localities, at elevations of 2750–2854 m on the eastern slopes of the Cordillera Occidental in southern Ecuador (Fig. 11.13).

Conservation Status

Gastrotheca litonedis is currently categorized as Endangered in the IUCN Red List. That assessment was based on two species, so the status of *G. litonedis* needs to be re-evaluated.

Etymology

The specific name is derived from the Greek *litos*, meaning "plain," and the Greek *nedys*, meaning "belly"; the name was applied to a species that characteristically has an unmarked venter (Duellman and Hillis, 1987).

Remarks

The photograph herein (Fig. 11.12A) is that of the holotype of *Gastrotheca litonedis*. The photograph published by Duellman and Hillis (1987:156, their Fig. 9), stated to be the holotype of *G. litonedis*, actually is a photo of *G. lojana* (KU 148794). After thorough review, all specimens, except the holotype, used in the description of *G. litonedis* actually represent an undescribed species.

Gastrotheca (*Duellmania*) *lojana* Parker

Gastrotheca marsupiata lojana Parker, 1932:25.—Holotype: BM 1947.2.31.13 from Loja, Provincia de Loja, Ecuador.
Gastrotheca monticola (in part)—Duellman and Hillis, 1987: 158.
Gastrotheca (*Duellmania*) *lojana*—Dubois, 1987:33.

Diagnosis

Adults of this species attain a maximum snout–vent length of 76.1 mm. The tibia length about 50% of the snout–vent length, and is slightly longer than the foot. The interorbital distance is about 65% the width of the upper eyelid. The skin on the dorsum is finely granular, not co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is about equal to the second. The discs on the fingers are about twice the width of the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and a point midway between the penultimate and distal subarticular tubercles on the fifth toe. The dorsum is green or tan, with darker paravertebral marks. Markings on the head consist of a pale labial stripe on the posterior half of the lip, and (usually) a dark interorbital bar connected to the paravertebral marks. The narrow pale dorsolateral stripe is fragmented. The flanks are dark brown, with pale spots; the venter is cream, with brown or gray flecks or spots.

In comparison with similar species in southern Ecuador, *Gastrotheca lojana* is most like *G. litonedis*. In *G. litonedis*, the first finger is slightly longer than the second; the first and second fingers are about equal in length in *G. lojana*. In *G. lojana*, the venter is cream, with brown or dark gray flecks or spots, whereas the venter is pale gray in *G. litonedis*. The groin and anterior and posterior surfaces of the thighs, as well as the ventral surfaces of the shanks, are dark brown with pale spots in *G. lojana*, whereas the flanks and anterior and posterior surfaces of the thighs are uniform in color in *G. litonedis*. The dorsal surfaces of Fingers I and II are cream with brown spots, in *G. lojana*, whereas they are green in *G. litonedis*. A fragmented cream supracloacal stripe is present in *G. lojana*, whereas the stripe is continuous in *G. litonedis*.

A distinctly different species, *G. pseustes*, occurs sympatrically with *G. lojana* in part of its range. This species differs from *G. lojana* by having coarsely granular skin on the dorsum, and blue tints in the axilla and groin. Another species in the Andes of southern Ecuador, *G. lateonota*, differs from *G. lojana* by having a smooth dorsum, lacking an interorbital bar, and having a truncate snout in profile.

Description

The following description is based on 36 specimens. The body is moderately robust. The maximum snout–vent length is 61.0 mm in males, and 76.1 mm in females. The head is slightly wider than long, and about as wide as the body. The snout is bluntly rounded in dorsal view, and is nearly truncate in profile. The canthus rostralis is angular in cross-section. The loreal region is barely concave; the lips are rounded. The top of the head is flat. The interorbital distance is about half again the width of the upper eyelid. The internarial area is slightly depressed. The nostrils are barely protuberant, and are directed laterally at a level just posterior to the anterior margin of the lower lip and at the terminus of the canthus rostralis. The diameter of the eye is equal to its distance from the nostril. The tympanum is vertically ovoid, and is separated from the eye by a distance much greater than the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately thick, and extends from the posterior corner of the eye to a point above the insertion of the forearm.

The arm is moderately robust, and lacks ulnar tubercles. The hand is moderate in size. The fingers are unwebbed. The discs on the fingers are small and round; the width of the disc on the third finger is notably less than the length of the tympanum. The relative lengths of the fingers are I > II < IV < III. The subarticular tubercles are moderately large and round. The supernumerary tubercles are small and few in number, occurring only on the proximal segments. The palmar tubercle is bifid; the prepollical tubercle is large, elongate, and ovoid; a patch of brown nuptial excrescences is present on the medial base of the thumb. The hind limb is moderately short and robust. The tibia length is about 50% of the snout–vent length; the foot length is about 45% of the snout–vent length. The heels lack calcars and tubercles. An outer tarsal fold is absent; an inner tarsal fold is present on the distal half of the tarsus. The inner metatarsal tubercle is rather small, ovoid, and visible from above; an outer metatarsal tubercle is absent. The toes are long. The relative lengths of the toes are I < II < III = V < IV. The toes are about one-third webbed, with no web between the first and second toes; the webbing formula for the other toes is **II**1½–3**III**2^-–3^+**IV**3^-–2**V**. The subarticular tubercles are moderately small and round; the supernumerary tubercles are small and present only on the proximal segments.

The texture of the skin on the dorsum of the head, body, and limbs is variably smooth to weakly granular. The skin on the flanks is smooth to weakly areolate. Tubercles are absent on the upper eyelids. The skin on the belly and ventral surfaces of the thighs is granular. Cloacal folds and tubercles are absent. The opening of the brood pouch is U-shaped, with the anterior border at the level of the sacrum. The dentigerous processes of the vomers are slightly inclined posteromedially, and are narrowly separated medially between the small round choanae. Each process bears five or six teeth.

COLOR IN PRESERVATIVE

The dorsum is dull bluish gray or brown, with darker paravertebral marks, which may be fragmented. Some specimens have dark brown to black flecks on the body, and most have distinct transverse bars on the limbs. Markings on the head consist of a white labial stripe that is narrower and, in some species, has dark flecks anteriorly; this stripe continues to the proximal anterior surfaces of the forearm. A broad interorbital bar, with a middorsal extension, connects to the paravertebral marks on the body. A dark canthal stripe and labial bars are absent. The flanks are dark gray, with small black and white spots. A white supracloacal stripe (usually fragmented) and white heel stripes are present. The groin, hidden surfaces of the thighs, and dorsal surfaces of the feet are mottled with black. Venter is dull cream, with dark gray markings varying from a few flecks to many spots or even to mottling.

COLOR IN LIFE

Three individuals (KU 138401–3) from Girón, Provincia de Azuay, Ecuador.—In the adult male the dorsum is pale yellowish green, with a beige dorsolateral stripe and a large bifurcate dorsal blotch that is dark yellowish green with a scattered bronze suffusion. The flanks and head are bronze beige, with a yellowish-green suffusion in the loreal region; the flanks also have a yellowish-green suffusion, and scattered dark grayish-blue blotches. The anterior surfaces of the thighs are yellowish beige, with gray blotches; the posterior surfaces of the thighs have a pale grayish-blue cast. The dorsal surfaces of the limbs have irregular green blotches. An adult female is similar, except for brighter grayish-blue blotches on the flanks and in axilla; the anterior and posterior surfaces of the thighs are bright grayish blue, with scattered yellowish-beige blotches; there are no dark blotches ventrally on the flanks. A juvenile has bright grayish-blue blotches on the flanks, and a grayish-blue tint on the posterior surfaces of the thighs; the anterior surfaces of the thighs are flesh colored (T. H. Fritts field notes, 6 June 1970).

Three adults from 5.5 km W Loja, Provincia de Loja, Ecuador.—One individual (KU 148549) is tan above, with a greenish suffusion dorsolaterally; the dorsolateral and labial stripes are bronze; the flanks and dorsal markings are dark brown. The upper thighs are bronze tan. The upper surfaces of the shanks and posterior surfaces of the thighs are green; the anterior surfaces of the thighs are dark brown. The throat is brown; the belly is brown and white; the ventral surfaces of the thighs are pinkish brown; the ventral surfaces of the shanks are bluish white. Another individual (KU 148550) is tan above, with brown markings (Fig. 11.14B); the facemask and anterior surfaces of the flanks are dark brown, and the labial stripe is creamy bronze. The anterior and posterior surfaces of the thighs are mottled dark brown and blue; the throat is dark gray; the belly is brown and white. The third individual (KU 148551) is dull green above, with dark brown markings and flanks; the groin, anterior and posterior surfaces of the thighs, and inner surfaces of the shanks are mottled dull blue and black. The throat is bronze brown; the venter is mottled brown and cream. The iris is bronze in all individuals (W. E. Duellman field notes, 23 July 1971).

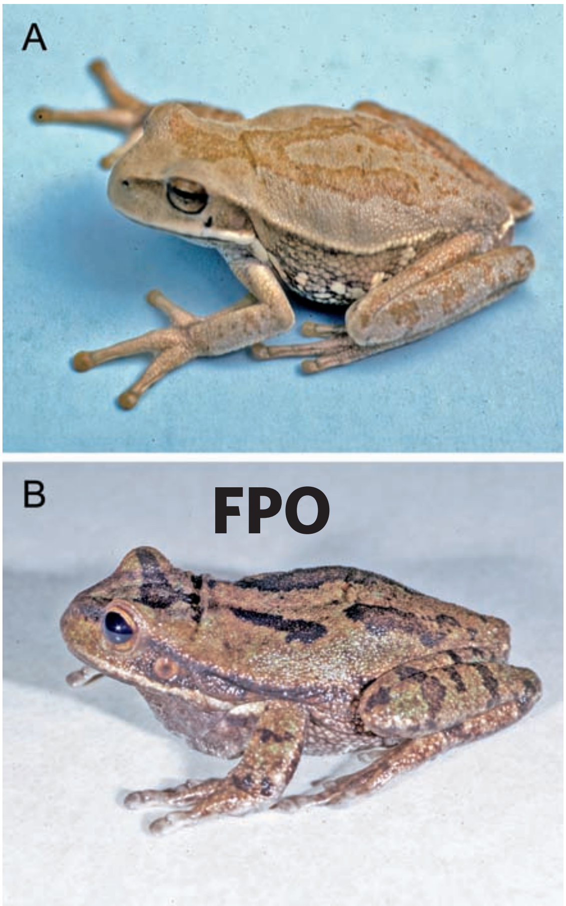

Fig. 11.14 *Gastrotheca lojana*. A: KU 142604, female, 65.4 mm SVL. B: KU 148550, male, 40.1 mm SVL. Both from 5.5 km W Loja, Loja, Ecuador. Photos by W. E. Duellman.

MEASUREMENTS

Females are noticeably larger than males (Table 11.7).

CRANIAL OSTEOLOGY

No skeletal preparations are available.

Life History

Gastrotheca lojana produces eggs that hatch as tadpoles in the brood pouch. Two females from the vicinity of Loja, Ecuador, had 128 and 96 eggs, respectively, in their brood pouches; the eggs were in Stages 23 and 30, with diameters of 3.7 mm.

Tadpoles

A series of tadpoles from 7.9 km W Loja, Provincia de Loja, Ecuador, contains individuals in Stages 35–41. A typical tadpole in Stage 38 (KU 203548) has a body length of 20.2 mm, and a total length of 45.8 mm. In dorsal view the body is ovoid, widest at about midlength; the snout is bluntly rounded. In profile the body is highest posteriorly, wider than high, and gradually inclined to a rounded snout. The throat is convex. The eyes are small, and are directed dorsolaterally. The interorbital distance is about one-third the width of the body at the level of the orbits. The nostrils are about midway between the eyes and the tip of the snout. The spiracular tube is short, and is attached to the body throughout its length. The spiracular opening is directed posteriorly on the ventrolateral surface of the body at a point about 50% of the length of the body. The cloacal tube is short, conical, and dextral, with a diagonal opening. The caudal musculature is moderately slender; it is not as high as the dorsal fin at midlength of the tail. The musculature terminates in a pointed tip just short of the margin of the caudal fin. The dorsal fin arises gradually from the proximal part of the caudal musculature. The height of the dorsal fin is slightly greater than that of the ventral fin at midlength of the tail; the fins terminate in a rounded tip.

The width of the oral disc is about one-third the width of the body. The disc is bordered laterally and

Table 11.7 Univariate statistics for adults of *Gastrotheca lojana*

	Males ($n = 24$)			Females ($n = 12$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length**	49.4	40.2–61.0	4.47	61.6	54.1–76.1	5.67
Tibia length**	25.2	19.8–31.1	2.91	31.2	27.4–36.5	3.22
Foot length**	22.2	17.9–26.6	2.03	28.0	22.8–35.5	3.54
Head length**	16.8	13.9–19.2	1.48	19.7	17.9–22.8	1.61
Head width**	18.7	15.4–22.1	1.84	22.0	19.4–24.2	1.35
Interorbital distance**	6.7	4.1–7.9	0.95	8.2	6.9–10.5	1.07
Eyelid width	4.3	3.5–5.3	0.45	4.4	3.7–5.4	0.40
Internarial distance**	3.0	2.3–3.7	0.38	3.7	3.2–4.1	0.23
Eye diameter**	4.9	3.4–5.7	0.51	5.6	5.0–6.3	0.34
Eye–nostril distance**	4.9	4.2–5.7	0.42	5.6	4.6–6.3	0.52
Orbit–jaw distance**	2.3	1.7–3.0	0.32	2.8	2.0–3.4	0.39
Nostril–jaw distance**	3.3	2.7–3.9	0.33	3.8	3.2–4.7	0.48
Tympanum diameter	3.4	2.8–4.1	0.38	3.5	2.9–5.0	0.58
Thumb length**	8.8	6.3–10.9	1.23	11.1	9.1–14.5	1.69
Third finger length**	15.4	12.3–19.5	1.76	18.7	9.2–24.4	3.62
Disc width**	2.6	2.0–3.8	0.37	3.2	2.4–4.2	0.65

**Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

ventrally by a single row of long pointed marginal papillae. There are two upper and three lower rows of labial teeth; the upper rows are slightly longer than the lower ones, and are subequal in length; the lower rows are progressively shorter; the second upper row and first lower row are interrupted medially. The upper jaw sheath is thick, and is broadly arch-shaped; the lower sheath is more massive, and is broadly V-shaped. Both sheaths bear low blunt serrations.

In preservative the body is dull brown. The skin on the venter is unpigmented. The caudal musculature is tan, with brown flecks. The fins are translucent, with brown flecks. In life the dorsum is black; the belly is gray (W. E. Duellman field notes, 10 March 1984). Tadpoles metamorphosed on 4 April 1984; the metamorphosing young were bright green.

Advertisement Call

Like other Andean species of *Gastrotheca*, the call consists of a low-pitched note, followed or not by two or three shorter notes.

Distribution and Ecology

Gastrotheca lojana has a broad distribution in the intermontane basins and adjacent Andean slopes in southern Ecuador, where it is known at elevations of 1700–3020 m (Fig. 11.15). The frogs have been found in a variety of microhabitats, including under rocks in pastures, in grassy vegetation, and along irrigation

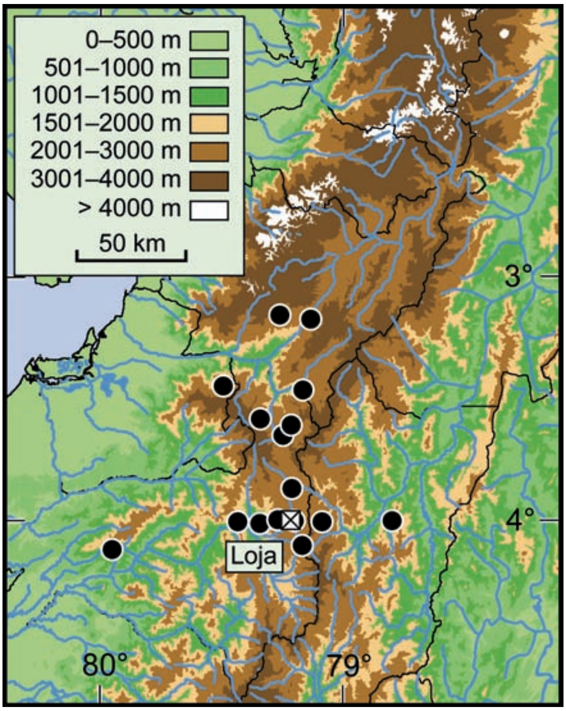

Fig. 11.15 Andean region of southern Ecuador, showing the localities of known occurrences of *Gastrotheca lojana*.

ditches. At some localities, especially in the Loja Basin, the frogs live in large *Agave*; they perch on, and call from, the leaves at night and retreat to the apices of the leaves by day.

Conservation Status

Gastrotheca lojana is categorized as Endangered in the IUCN Red List, because of urban growth and pesticide contamination,

Etymology

The specific name *lojana* refers to the city of Loja and the province of the same name in southern Ecuador, where the species was first discovered.

Remarks

The taxonomic status of *Gastrotheca lojana* has had a whirlwind history. Parker (1932) named *G. lojana* as a subspecies of *G. marsupiata*, a name that he applied to frogs now known as *G. riobambae*. Duellman (1974) recognized *G. lojana* as a species distinct from *G. riobambae* and similar to *G. monticola*, which Parker (1932) also considered to be a subspecies of *G. marsupiata* [= *G. riobambae*]. Duellman and Hillis (1987) noted that there were no immunological differences between *G. lojana* and *G. monticola*; therefore they placed *G. lojana* Parker, 1932, in the synonymy of *G. monticola* Barbour and Noble, 1920. Most recently, Duellman et al. (2014) showed that Ecuadorian populations were genetically distinct from *G. monticola* in northern Peru, and these authors recognized *G. lojana* as a distinct species.

Gastrotheca (*Duellmania*) *monticola* Barbour and Noble

Gastrotheca monticola Barbour and Noble, 1920:426.—Holotype: MCZ 5290 from Huancabamba, Región de Piura, Peru.

Gastrotheca (*Duellmania*) *monticola*—Dubois, 1987:33.

Diagnosis

Adults of this species attain a maximum snout–vent length of 64.7 mm. The tibia length is no more than 55% of the snout–vent length, and is about the same length as the foot. The interorbital distance is much wider than the upper eyelid. The skin on the dorsum is shagreen to finely granular, not co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first and second fingers are about equal in length. The discs on the fingers are much wider than the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends maximally to the penultimate subarticular tubercle on the fourth toe and nearly to the distal subarticular tubercle on the fifth toe. The dorsum is green or brown, usually with a darker middorsal blotch or paravertebral marks. Markings on the head usually consist of a dark canthal stripe and pale labial stripe. A pale dorsolateral stripe usually is present. The flanks and the anterior and posterior surfaces of the thighs are pale yellow or pale green, with black spots or mottling; the venter is cream, with dark flecks or spots.

Gastrotheca monticola most closely resembles four other species in northern Peru. In contrast to the slightly larger *G. monticola*, *G. aratia* usually lacks a pale supracloacal stripe and black spots on the flanks and the anterior and posterior surfaces of the thighs. *G. aguaruna* differs by being much smaller (females to 51 mm) than *G. monticola*, and also by lacking a pale supracloacal stripe and black spots on the flanks and the anterior and posterior surfaces of the thighs. *G. dysprosita* is like *G. monticola* in having a bluntly rounded snout in profile, but differs from *G. monticola* by having a green dorsum with a narrow yellow middorsal stripe, and green flanks with small yellow spots; furthermore, *G. dysprosita* lacks a dark canthal stripe and pale labial stripe. *G. lateonota* is like *G. monticola* in size and in most proportions, but *G. lateonota* differs from *G. monticola* by having a truncate snout in profile, smooth skin on the dorsum, and a nearly uniformly grayish-brown venter. Among the six other species of *Gastrotheca* in the Andes in northern Peru, *G. peruana*, *phalarosa*, and *phelloderma* have pustular skin on the dorsum, and *G. ossilaginis* has the skin on the head co-ossified with the dermal elements of the skull. Two other species produce eggs that undergo direct development. Of these, *G. abdita* has an acuminate snout in dorsal view, and *G. galeata* has a spatulate labium.

Description

The following description is based on 43 specimens. The body is robust. In a series from Pomcochas, Región de Amazonas, Peru, the maximum snout–vent length is 55.7 mm in males, and 66.3 mm in females. The head is noticeably wider than long, and as wide as the body. The snout is rounded in dorsal view, and is bluntly rounded to truncate in profile. The canthus rostralis is rounded in cross-section. The loreal region is barely concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 175% of the width of the upper eyelid. The internarial area is flat. The nostrils are slightly protuberant laterally, below the anterior terminus of canthus rostralis at the level of the anterior margin of the lower jaw. The diameter of the eye is slightly greater than its distance from the nostril. The tympanum is vertically ovoid, and is separated from the eye by a distance slightly greater than the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is rather weak, extends from the posterior corner of the orbit to a point above the insertion of the arm, and barely overlaps the upper edge of the tympanum.

The arm is moderately robust, and lacks ulnar tubercles. The hand is moderate in size. The fingers are unwebbed. The discs on the fingers are large, much wider than the discs; the width of the disc on the third finger is equal to the length of the tympanum. The relative lengths of the fingers are I = II < IV < III. The subarticular tubercles are moderately large and rounded; none are bifid. The supernumerary tubercles are small, round, and numerous on the proximal segments. The palmar tubercle is low and bifid; the prepollical tubercle is elongately elliptical; the thumb bears nuptial excrescences in breeding males. The hind limb is moderately slender. The tibia length is slightly more than 50% of the snout–vent length; the foot length is about 46% of the snout–vent length. The heel lacks a calcar or tubercle; an outer tarsal fold is absent. The inner tarsal fold is distinct on the distal two-thirds of the tarsus. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is elongately elliptical, and is not visible from above. The toes are long. The relative lengths of the toes are I < II < III < V < IV. The toes are about two-thirds webbed; the webbing formula is **I**2—2**II**2^{-}—3**III**1½—(1–2)**IV**(1–2)—(1½–2)**V**. The subarticular tubercles are small and round; the supernumerary tubercles are minute, round, and present only on the proximal segments.

The skin on the dorsum is shagreen to finely granular; the skin on the ventral surfaces of the shanks is smooth; the other ventral surfaces are granular. Cloacal tubercles and folds are absent. The opening of brood pouch is narrowly U-shaped, with the anterior border at the posterior edge of the sacrum. The dentigerous processes of the vomers are transverse, and are narrowly separated medially at the level of the posterior margins of the small round choanae. Each process bears five to seven teeth.

COLOR IN PRESERVATIVE

The dorsum is dull bluish gray or tan, with dark markings consisting of a middorsal mark from the occiput to the sacrum, or being completely separated on the occiput into paravertebral marks or blotches. The dorsal surfaces of the shanks are uniformly bluish gray or tan, and usually have darker transverse bars. A pale dorsolateral stripe and a pale supracloacal stripe are present in most individuals. The flanks are dark bluish gray or brown. The anterior and posterior surfaces of the thighs are dull bluish gray, with black spots. The ventral surfaces of the body and shanks are pale cream, with dark spots in nearly all individuals; the vocal sac is dark gray. A dark canthal stripe and pale labial stripe are present in most specimens.

COLOR IN LIFE

The dorsal coloration is variable from green to tan, with darker green or brown markings (Fig. 11.16). The distinctiveness and tones of the colors on the venter and hidden surfaces are variable, as illustrated by the following examples.

A series (KU 181742–70) from Pomacochas, Región de Amazonas, Peru.—The dorsum is bright green in most individuals, but is tan in juveniles and in one adult male. The flanks are green, with black spots; the anterior and posterior surfaces of the thighs, ventral surfaces of the shanks, and hidden surfaces of the feet are yellow to yellowish green, with black spots. A tint of blue is in the groin in some individuals. The labial, supracloacal, and tarsal stripes are creamy bronze; the upper arms, dorsal surfaces of the digits, and dorsolateral stripe (present in a few) are bronze tan. The venter is creamy gray, with gray-brown spots. The iris is deep bronze, with black reticulations. In calling males, the throat is coppery bronze medially, and green to yellowish green laterally (W. E. Duellman field notes, 4 March 1979).

Four specimens (KU 219769–70, MUSM 15420–21) from 4 km N Huancabamba, Región de Piura, Peru.—Included among them is a female (KU 219769) with a pale green dorsum, a bronze-brown bar between the eyes, and a broad middorsal stripe (bronze-brown-green) that bifurcates at midbody and rejoins at the opening to the pouch. The flanks are bronze copper, with some green spots, and are separated from the dorsum by a dark brown line. The lips are yellow; the iris is gold, with black reticulations and a dark horizontal median band. The tympanum is copper. The venter is pinkish white. There are green spots in the inguinal region. The anterior surface of the thigh has black spots; the posterior surface is light green, with dark green spots (E. R. Wild field notes, 9 July, 1991).

MEASUREMENTS

Females are significantly larger than males in overall size, but the means of the measurements of some characters of the head are not significantly different (Table 11.8).

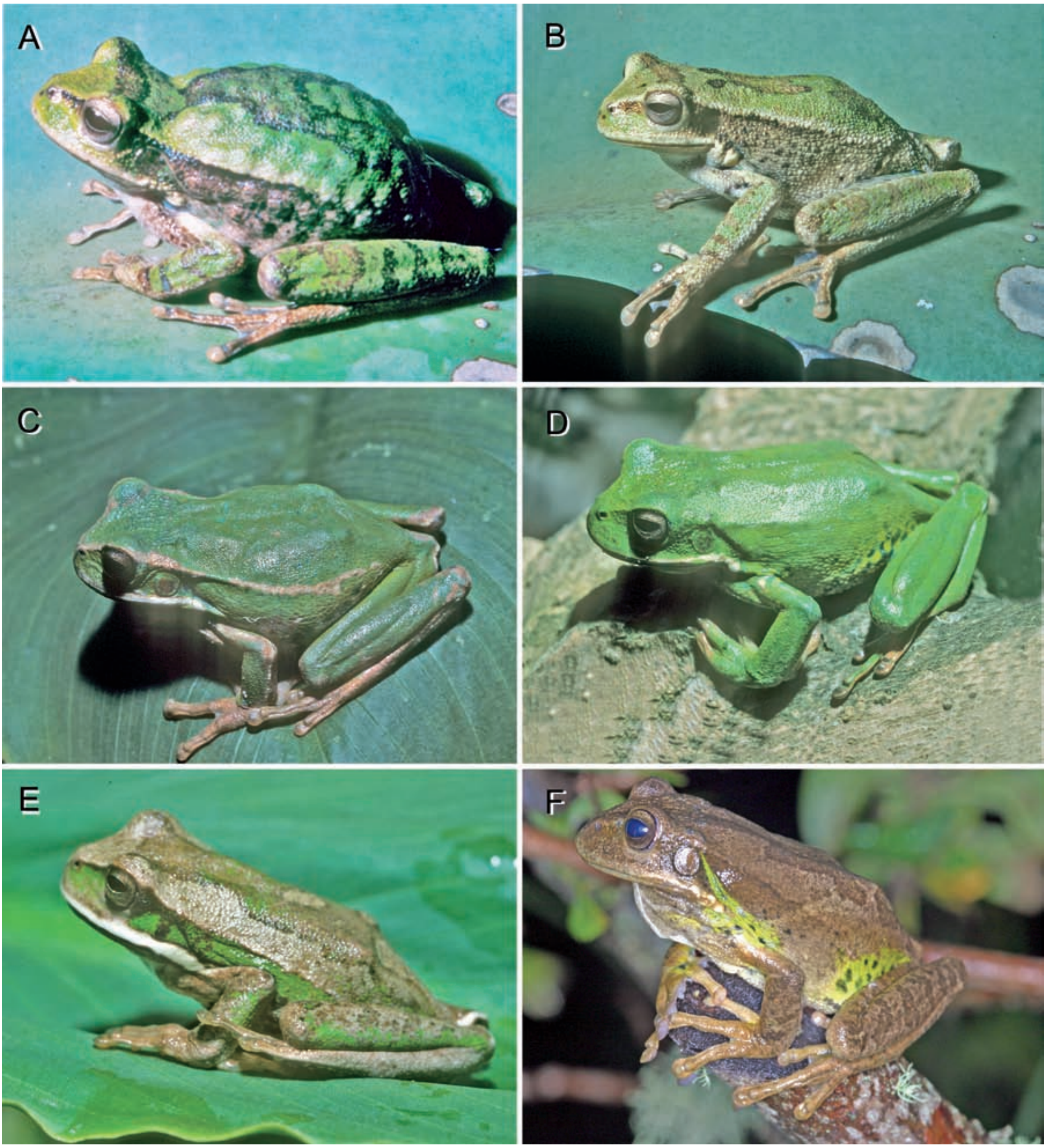

Fig. 11.16 Diversity of color patterns in *Gastrotheca monticola* in northern Peru. A: KU 219769, female, 68.1 mm SVL, 4 km N Huancabamba, 1900 m, Piura. B: KU 219770, female, 57.7 mm SVL, same locality. C: KU 181742, male, 54.3 mm SVL, Pomacochas, 2150 mm, Amazonas. D: KU 212033, male, 51.5 mm SVL, same locality. E: KU 212032, juvenile, 30.8 mm SVL, same locality. F: MHNC 6742, male, 56.3 mm SVL, Kuelap, 2920 m, Amazonas. Photos by E. R. Wild (A and B), W. E. Duellman (C–E), and J. C. Chaparro (F), KUDA.

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous semicoarse shallow pit-and-ridge pattern. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete medial articulation; each bears wide supraorbital and otic flanges. The temporal arcade is complete. The frontoparietal

Table 11.8 Univariate statistics for adults of *Gastrotheca monticola* from Pomacochas, Peru

	Males (n = 11)			Females (n = 16)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length*	51.7	49.0–55.7	2.62	58.4	48.0–66.3	5.11
Tibia length*	26.9	24.2–29.7	1.55	29.8	25.4–33.0	2.19
Foot length*	22.9	20.4–24.7	1.55	25.7	21.2–29.8	2.40
Head length*	16.5	15.1–18.0	0.87	18.6	15.2–20.4	1.53
Head width*	19.2	17.2–21.0	1.19	21.9	17.8–29.8	2.69
Interorbital distance*	6.7	5.8–7.7	0.64	7.7	6.4–9.0	0.73
Eyelid width	4.0	3.2–4.6	0.45	4.4	3.8–5.1	0.38
Internarial distance*	3.5	3.2–3.8	0.19	3.9	3.3–4.6	0.30
Eye diameter	5.2	4.7–5.7	0.34	5.6	5.3–6.2	0.38
Eye–nostril distance*	4.8	4.4–5.4	0.31	5.6	5.3–6.2	0.38
Orbit–jaw distance	2.5	2.2–2.7	0.16	2.7	2.4–3.3	0.31
Nostril–jaw distance*	3.3	2.9–3.9	0.30	3.9	3.0–4.6	0.46
Tympanum diameter	2.8	2.2–3.2	0.39	3.0	2.6–3.4	0.27
Thumb length*	9.2	7.4–10.3	0.75	10.6	8.5–12.2	1.18
Third finger length*	16.5	14.9–17.9	1.07	18.7	15.7–21.3	1.76
Disc width	2.7	2.3–2.9	0.23	3.1	2.5–3.8	0.40

*Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

covers the entire otic region, and is fused to the epiotic eminences; hence the carotid canal is closed, and exits the skull posteriorly adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for more than three-fourths the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The postorbital process of the maxilla is low but distinct, and has a narrow articulation with the slender zygomatic process of the squamosal. The head of the squamosal bears a wide crest; the otic plate articulates with and narrowly overlaps the crista parotica. The dorsal part of the stapedial footplate is two to three times the length of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are widely separated medially; each bears a low irregular ridge ventrally. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a long blunt-tipped process on the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located between the middle quadrants of the choanae.

Life History

Gastrotheca monticola produces eggs that hatch as tadpoles in the brood pouch. Three individuals collected on 4 March 1979 at Pomacochas, Región de Amazonas, Peru, respectively had 169, 97, and 66 eggs in their brood pouches; the eggs were in Stages 18, 22, and 30, with diameters of 3.6, 4.5, and 4.9 mm.

Tadpoles

A series of tadpoles from near the type locality contains individuals in Stages 30–41. A typical tadpole in Stage 36 (KU 181874) has a body length of 21.3 mm, and a total length of 49.6 mm. In dorsal view the body is ovoid, widest at about two-thirds the length of the body. The snout is bluntly rounded in dorsal view. In profile the body is highest posteriorly, and is gradually inclined to a rounded snout. The body is slightly wider than high. The throat is convex. The eyes are small, and are directed dorsolaterally. The interorbital distance is about one-third the width of the body at the level of the orbits. The nostrils are about midway between the eyes and the tip of the snout. The spiracular tube is short, and is attached to the body throughout its length. The spiracular opening is directed posteriorly on the ventrolateral surface of the body at a point about 55% of the length of the body. The cloacal tube is short, conical, and dextral, with a diagonal opening.

The caudal musculature is moderately slender; it is not as high as the dorsal fin at midlength of the tail. The musculature terminates in a pointed tip just short of the margin of the caudal fin. The dorsal fin arises gradually from the proximal part of the caudal musculature. The height of the dorsal fin is slightly greater than that of the ventral fin at midlength of the tail; the fins terminate in an acutely rounded tip.

The width of the oral disc is about one-third the width of the body. The disc is bordered laterally by a single row of long pointed marginal papillae, and ventrally by two rows of alternating long pointed papillae. There are two upper and three lower rows of labial teeth. The upper rows are slightly longer than the lower ones, and are subequal in length. The lower rows are progressively shorter; the second upper row and first lower row are interrupted medially. The upper jaw sheath is thick and broadly arch-shaped; the lower sheath is more massive, and is broadly V-shaped. Both sheaths bear low blunt serrations.

In preservative the body is dull brown. The skin on the ventrolateral surfaces and the venter is unpigmented. The caudal musculature is cream, with a broad brown streak along the entire upper edge, and a narrower brown streak on the proximal third of the lower edge. The fins are translucent, with fine brown reticulations. In life the body and tail are pale olive tan; the belly is gray. The dorsal and ventral edges of the proximal caudal musculature are dark brown. The iris is creamy yellow (W. E. Duellman field notes, 26 February 1979).

Three individuals in Stage 41 have snout–vent lengths of 18.9, 20.7, and 20.9 mm and tail lengths of 20.1, 23.3, and 26.8 mm, respectively.

Advertisement Call

The call consists of a single low pulsed note, followed or not by two or three much shorter notes. The call of *Gastrotheca monticola* described by Sinsch and Juraske (2006) is of a frog of unknown provenance, and certainly is not that of *G. monticola*.

Distribution and Ecology

In the Huancabamba Depression, *Gastrotheca monticola* inhabits subhumid intermontane basins and the valleys of Río Marañón and Río Zamora at elevations of 1000 to 2700 m. In the northern part of the Cordillera Occidental in Peru, it occurs at elevations of up to 3350 m, and in the northern part of the Cordillera Central in Peru, up to elevations of 3440 m (Fig. 11.17). In the Cordillera de Huancabamba in northern Peru, *G. monticola* inhabits tropical dry forest at elevations below 1400 m, whereas *G. galeata* and *G. lateonota* inhabit cloud forest at higher elevations.

The species has been found in semiarid scrub forest characterized by thorny legumes and cacti, in cloud forest, and in subpáramo. Individuals have been found on low bushes and on *Agave* at night; and by day in bromeliads, in grassy drainage ditches, under rocks and clods of dirt, amid deep moss, and in *Agave*. Tadpoles have been found in shallow grassy temporary ponds.

Conservation Status

In the IUCN Red List, *Gastrotheca monticola* is categorized as being of Least Concern. Aguilar et al. (2012) suggested that the species may become endangered within mineral concessions in northern Peru.

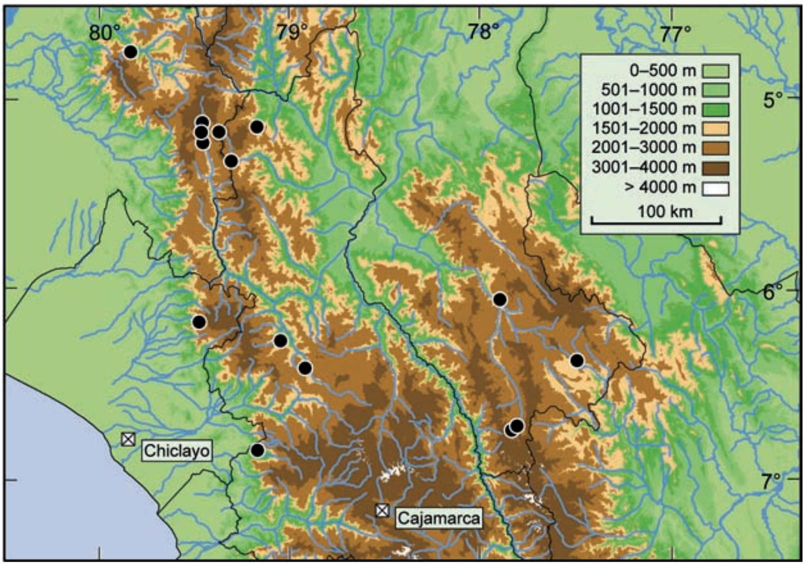

Fig. 11.17 Andean region of northern Peru, showing the localities of known occurrences of *Gastrotheca monticola*.

Etymology

The specific name is derived from the Latin *montis*, meaning "mountain," and the Latin *icola*, meaning "resident." The name refers to this species' habitation in mountains.

Remarks

Collections of frogs made in the Andes in northern Peru in 1979 and 1989 by Duellman and his field companions contained numerous specimens that were referred to *Gastrotheca monticola*. These frogs displayed considerable variation in color pattern and few differences in morphology. Consequently, all were considered to belong to a single species, but Duellman (2013) recognized two specimens with a distinctive color pattern to be a new species, *G. dysprosita*. Subsequently, Pablo Venegas collected additional specimens in northern Peru. DNA extracted from tissues obtained by Duellman and by Venegas clearly showed that what had been considered to be a single species actually was three species in two different clades: *G. monticola* and two new species, *G. aguaruna* and *G. aratia* (Duellman et al., 2014). Furthermore, they showed that Ecuadorian populations that had been referred to *G. monticola* were specifically distinct genetically; these populations were referred to *G. lojana* Parker, 1932, a change that was substantiated by the more extensive study by Carvajal-Endara et al. (2014).

Gastrotheca (*Duellmania*) *nicefori* Gaige

Gastrotheca nicefori Gaige, 1933:1.—Holotype: UMMZ 73242 from Pensilvania, Departamento de Caldas, Colombia.

Gastrotheca medemi Cochran and Goin, 1970:172.—Holotype: UMMZ 123068 from Cano Guapayita, 400 m, Serranía de la Macarena, Departamento de Meta, Colombia. Synonymy fide Duellman, 1989:109.

Gastrotheca nicefori descampsi Lutz and Ruíz-C., 1977: 12.—Holotype: ICN 318 [now lost] from Chorvalí, San Farncisco [= Francisco], "beyond the Valle de Sibundoy," Departamento de Putumayo, Colombia. Synonymy fide Duellman, 1989:109.

Gastrotheca yacambuensis Yústiz, 1978:87.—Holotype: MBUCV 6015 from Quebrada El Cedral, 1700 m, Parque Nacional de Yacambú, S slope Sierra de Portuguesa, Estado Lara, Venezuela. Synonymy fide Duellman, 1989: 109.

Gastrotheca (*Opisthodelphys*) *medemi*—Dubois, 1987:31.

Gastrotheca (*Opisthodelphys*) *nicefori*—Dubois, 1987:31.

Gastrotheca (*Opisthodelphys*) *yacambuensis*—Dubois, 1987:31.

Gastrotheca nicefori—Duellman, 1989:108.

Diagnosis

This large species attains a maximum snout–vent length of 81.2 mm. The tibia length is more than 55% of the snout–vent length, and is slightly longer than the foot. The interorbital distance is about twice the width of the upper eyelid. The skin on the dorsum is areolate, co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel is devoid of a calcar or tubercle. The tympanic annulus is smooth. The first finger is longer than the second. The discs on the fingers are much wider than the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends maximally to a point midway between the antepenultimate and penultimate subarticular tubercles on the fourth toe and the distal subarticular tubercle on the fifth tow. The dorsum is tan or gray, usually with a dark blotch or spots. Markings on the head consist only of a narrow pale labial stripe in some individuals. A pale dorsolateral stripe is absent. The flanks are gray, with or without pale or dark spots. The venter is gray or brown, with or without dark spots or flecks.

Gastrotheca nicefori is one of five species of the genus having a casqued co-ossified skull with a transverse occipital ridge. Of these, *G. galeata* differs by having a depressed head with flared lips. *G. megacephala* and *G. prasina* differ by having the first finger much longer than the second, finely granular skin on the dorsum, and a truncate snout (as opposed to inclined) in profile. *G. weinlandii* differs by having the first finger much longer than second, a calcar on the heel, a granular tympanic annulus, a narrower interorbital region (about 150% of the width of the upper eyelid), and a dorsal pattern of diagonal dark streaks. *G. ovifera* differs in having dorsal projections on the posterior margin of the skull table, and vertical black bars in the groin.

Description

The following description is based on 57 specimens. The body is robust; the maximum snout–vent length is 74.7 mm in males, and 81.2 mm in females. The head is slightly wider than long, but not as wide as the body. The snout is bluntly rounded in dorsal view, and is inclined from the nostrils to the tip in profile. The canthus rostralis is angular in cross-section, and is slightly elevated. The loreal region is concave; the lips are slightly flared. The top of the head is depressed. The interorbital distance is about 200% of the width of the upper eyelid. The internarial area is flat. The nostrils are slightly protuberant, and are directed anterodorsally at the terminus of the canthus rostralis at a point slightly posterior to the anterior margin of the lower lip. The diameter of the eye is about equal to its distance from the nostril. The tympanum is round, and is separated from the eye by a distance about 1.5 times the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is heavy, bony anteriorly, extends onto the flank, and obscures the upper part of the tympanum.

The arm is moderately robust, and lacks ulnar tubercles. The hand is moderate in size. The fingers are moderately long, and bear large round discs; the width of the disc on the third finger is much greater than the length of the tympanum. The relative lengths of the fingers is I > II < IV < III. The fingers are unwebbed. The subarticular tubercles are large and round; none are bifid. The supernumerary tubercles are subconical. The palmar tubercle is bifid; the prepollical tubercle is elliptical; the thumb bears brown or black nuptial excrescence in males. The hind limbs are robust. The tibia length is about 51% of the snout–vent length; the foot length is about 46% of the snout–vent length. The heel lacks calcars or tubercles; tarsal tubercles are absent. The inner tarsal fold is low, and is shallowly scalloped on the distal two-thirds of the tarsus. The inner metatarsal tubercle is broadly elliptical, and is not visible from above; the outer metatarsal tubercle is small and subconical. The toes are moderately long. The relative lengths of the toes are I < II < III = V < IV. The toes are about one-third webbed; the webbing formula is **I**(2–2^{+})—(2–2½)**II**2^{-}—3^{-}**III**2^{-}—(2½–3) **IV**(2½–3)—(1–2)**V**. The subarticular tubercles are large and round; the supernumerary tubercles are low and diffuse.

The skin on the dorsum of the body is smooth (19%), areolate (79%), or granular (2%); the skin on the head is granular, and in adults is completely co-ossified with the underlying cranial elements; the skin on the flanks is smooth to weakly areolate; the skin on the belly and proximal ventral surfaces of the thighs is coarsely granular; the other ventral surfaces are smooth. A low transverse occipital ridge is present. Small conical tubercles are present in the temporal region; cloacal folds and tubercles are absent. The opening of the brood pouch is narrowly U-shaped, with the anterior margin at the level of the sacrum. The dentigerous processes of the vomers are transverse, and are narrowly separated medially at the level of the posterior margins of the choanae. Each process bears six to nine teeth.

COLOR IN PRESERVATIVE

The dorsum is pale tan to gray; the flanks are darker brown to black; the venter is dark gray. In most specimens a narrow creamy tan line separates the dorsal and lateral colors. A pale labial stripe is present in about half (54%) of the specimens. A dark interorbital bar and canthal stripe are absent; a dark postorbital bar is present. The dorsum is uniformly pale (23%), pale with dark flecks (26%), or pale with dark spots (51%); of 29 specimens in latter category, 41% have a tendency for a large middorsal mark. The dorsal surfaces of the shanks are uniform (56%), or have dark spots (14%) or diffuse transverse bars (30%). The flanks are uniformly pale (30%), uniformly dark (19%), pale with dark spots (32%), or dark with pale spots (19%). The anterior surfaces of the thighs are uniformly gray or brown (14%), or also have darker mottling (86%). The posterior surfaces of the thighs are uniformly dark (48%), uniformly pale (7%), dark with pale spots (14%), or pale with dark spots (5%) or vertical bars (26%). The venter is uniformly dark gray or brown (76%), uniformly tan (2%), or tan with dark spots (12%) or flecks (10%). The outer toes are colored like the inner ones.

COLOR IN LIFE

The coloration of *Gastrotheca nicefori* is as variable in life as it is in preservative (Fig. 11.18), as is illustrated by the following notes taken on living individuals.

Two adults (KU 169416–17) from the Parque Arqueológica San Agustín, Departamento de Huila, Colombia.—The female (KU 169416) is bronze tan above, with a dull brown postorbital bar extending onto the flanks. The throat is pinkish bronze; the rest of the venter and hidden surfaces of the limbs are pale gray, with dark gray reticulations; the iris is pale pinkish bronze. The male (KU 169417) has a grayish-tan dorsum, with dark brown flecks; the venter is dull gray, with dark brown spots (W. E. Duellman field notes, 26 May 1975).

Four individuals (ICN 6397–400) from 7 km NW of San José de Isnos, Departamento de Huila, Colombia.—The head is bronze brown. The middle of the back is slightly grayish (orange tan with black spots in ICN 8398). A dark brown postorbital bar extends onto the arm. The vocal sac is dirty brown; the rest of the venter is brownish gray. The hidden surfaces of the limbs are pale grayish tan, with a hint of blue; the posterior surfaces of the thighs are almost brown in two individuals (ICN 6399–400). The thumb pad is brown to black. The iris is gray, with a tan wash and black reticulations (gray with brown reticulations and a cream ring around the pupil in ICN 6398) (J. D. Lynch field notes, 26 July 1980).

Three adults (WWL 1156–58) from Parque Zoologico Santa Cruz, Departamento de Cundinamarca, Colombia.—The dorsum is yellowish tan, pinkish tan,

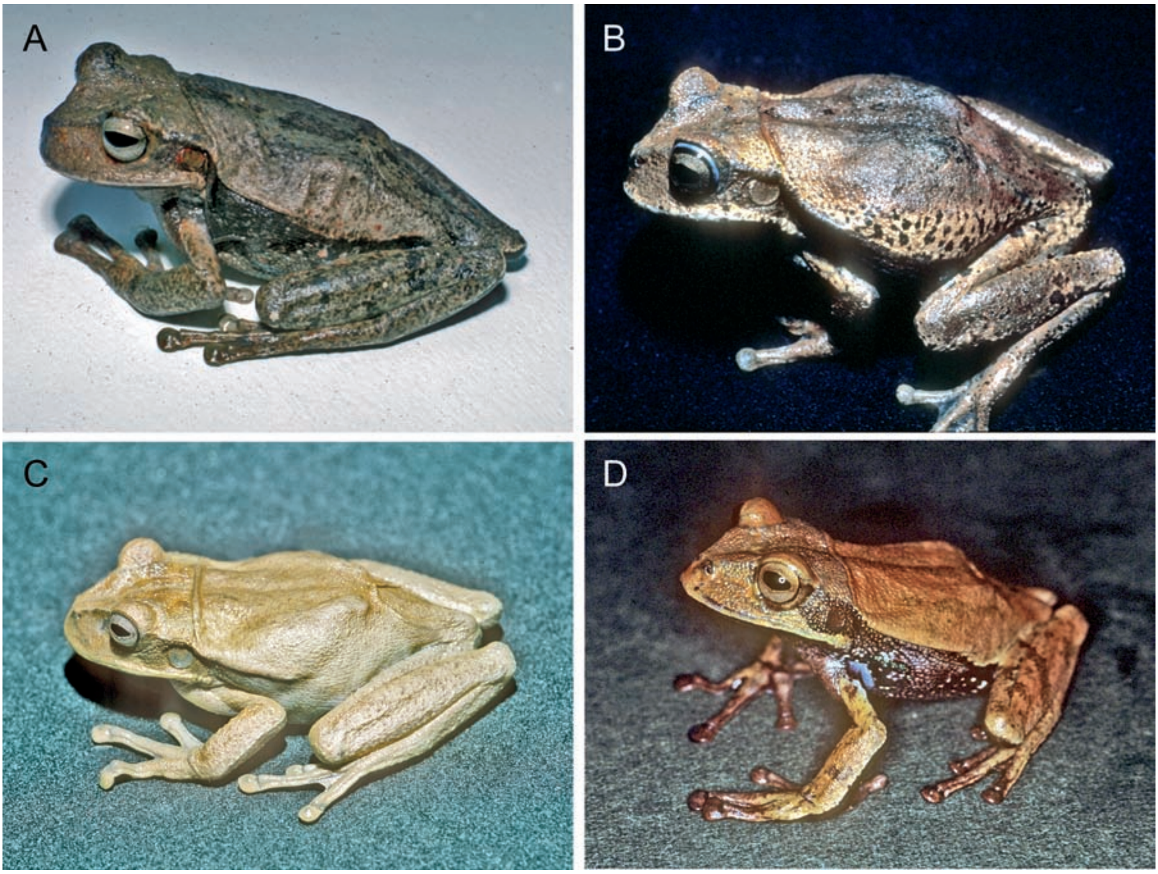

Fig. 11.18 *Gastrotheca nicefori*. A: KU 111991, male. 65.7 mm SVL, ridge between Río Jaqué and Río Imamadó, Darién, Panama. B: KU 181071, male, 60.9 mm SVL, 1 km S Delicias, 1910 m, Táchira, Venezuela. C: KU 169416, female, 56.3 mm SVL, Parque San Agustín, 1750 m, Huila, Colombia. D: ICN 4782, female, 71.4 mm SVL, Portachuela, 1400 m, Meta, Colombia. Photos by C. W. Myers (A), W. E. Duellman (B and C), and J. D. Lynch (D), KUDA.

or soft gray, with or without several widely scattered irregular brown spots. Some individuals have faint bars on the limbs. The flanks and hidden surfaces of the limbs are uniformly grayish brown; the venter is uniformly chocolate brown to sooty gray; the iris is reticulated with pinkish gold (W. W. Lamar field notes, 6 December 1979).

Two individuals (WWL 932–33) from Vereda de Portachuelo, Departamento de Meta, Colombia.—An adult (WWL 932) has a fleshy tan dorsum, with scattered paler blotches; the flanks and hidden surfaces of the limbs are mottled gray and pinkish flesh. The venter is yellowish tan; the palmar and plantar surfaces are pinkish gray. The iris is tan, with narrow radiating black lines. A juvenile (WWL 933) has a yellowish-tan dorsum, with a darker canthal region and flanks, and vague dark areas on the dorsum. The inguinal region and hidden surfaces of the limbs are saffron yellow; the digits are orange yellow. The margin of the upper lip is white. The cloacal region is dark brown, with a greenish-white transverse stripe above the vent. The venter is saffron yellow, most intense on the legs; the chest is somewhat whitish. The margin of the lower lip and lateral edges of the belly are greenish gray. The iris is metallic yellow brown, with a coppery ring around the pupil (W. W. Lamar field notes, 8 July 1979).

An adult (KU 101538) from Cerro de Cituro, Provincia de Darién, Panama.—The dorsum is yellowish brown, with a few blackish-brown spots; an indefinite yellow line separates the dorsal color from the darker flanks. The venter, flanks, and hidden surfaces of the thighs are dark brown, darkest on the flanks and posterior surfaces of the thighs. There is no blue. The iris is pale brown (C. W. Myers field notes, 24 January 1966).

AMNH 90986–87 from Cerro Tacarcuna, Provincia de Darién, Panama.—The dorsum is pale brown or orange brown; the posterior surfaces of the thighs and the entire venter are blackish brown, except for turning gray on the undersides of the digits. The iris is pale brown, with black flecks around the pupil (AMNH 90986) or with sparse dark venation (AMNH 90987) (C. W. Myers field notes, 1–7 February 1975).

An adult (KU 181071) from 11 km S Delicias, Estado Táchira, Venezuela.—The dorsum is pale brown, becoming yellowish tan laterally, with black flecks; the flanks and hidden surfaces of the thighs are dark brown, with black flecks; the venter is grayish brown, with black flecks. The iris is pale bronze, with fine black reticulations (W. E. Duellman field notes, 4 February 1979).

Color photographs of the holotype of *Gastrotheca yacambuensis* (MBUCV 6015) provided by Enrique Yústiz show the dorsum to be bronze tan, with minute black flecks; the flanks are pale brown, with a blue tint in the axilla and groin. The venter is gray. The iris is bronze tan, with fine black flecks.

Diurnal-nocturnal metachrosis is evident from the following field notes.

An adult (KU 101538) from Cerro de Citurio, Provincia de Darién, Panama.—By day all exposed dorsal surfaces were silvery gray, with white and a few brownish spots sparsely and irregularly scattered on the dorsum. An ill-defined bronze stripe extends from the eye to the arm; a pale pink line extends from above the tympanum to the groin. Extensive areas in the axilla and undersides of arm, in the groin and anterior surfaces of the thigh, on the posterior surfaces of the thigh, ventral surface of the shank, and inner side of the top of the foot and the webbing, as well as dark striations on the anterior part of the flank are all dark blue. The throat and adjacent part of the chest are silvery gray; the rest of the venter is darker gray. The iris is pale gray. By night the dorsum became brown; the white spots and pink line became pale brown; the brown spot that had been present by day became blackish brown. The ventral surfaces also darkened. The iris changed to pale grayish brown (C. W. Myers field notes, 21 January 1966).

An adult (KU 111991) from Serranía del Sapo, Provincia de Darién, Panama.—The dorsum was pale grayish brown at night; it changed to medium brown by day. The flanks, groin, and hidden surfaces of the thighs are dark brown, almost black on the thighs, with small touches of pink on the flanks and the barest tinge of blue on the posterior surfaces of the thighs. The venter is pale dirty grayish brown. The iris is pale grayish brown, with fine black reticulations (C. W. Myers field notes, 23 April 1967).

One individual (KU 133392) from 3 km NE Boconó, Estado Trujillo, Venezuela.—It was pale whitish gray dorsally when found sleeping by day; subsequently, the dorsum became brown. The labial stripe is creamy white. The belly is grayish tan; the ventral surfaces of the hind limbs are black. The iris is silvery gold, with black reticulations (S. R. Edwards field notes, 17 June 1970).

MEASUREMENTS

In most measurements, females are significantly larger than males (Table 11.9).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous fine pit-and-ridge pattern. The nasals articulate medially, and are fused to one another and the sphenethmoid posteriorly; posterolaterally, the nasals articulate at the anterolateral margin of the frontoparietals. The frontoparietals have a complete articulation medially; each bears wide supraorbital and otic flanges. The temporal arcade is complete. The frontoparietal covers the entire otic region, and is partially fused to the epiotic eminences; hence the carotid canal is only partly closed, and exits the skull posteriorly adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for more than three-fourths the length of the rostrum. The pars facialis is not distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The postorbital process of the maxilla is absent or scarcely evident; the wide zygomatic process of the squamosal articulates with the margin of the pars facialis of the maxilla. The head of the squamosal bears a wide crest that articulates with the otic flange of the frontoparietal; the otic plate of the squamosal articulates with and narrowly overlaps the crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in size, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are narrowly separated medially; the venters are smooth. The pterygoid articu-

Table 11.9 Univariate statistics for adults of *Gastrotheca nicefori*

	Males ($n = 23$)			Females ($n = 16$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length*	63.5	52.1–74.7	5.45	69.0	60.0–82.2	7.39†
Tibia length**	32.4	26.3–40.8	3.46	35.7	28.2–44.1	4.16
Foot length**	28.6	23.6–35.9	2.84	32.2	26.8–37.8	3.41
Head length**	24.7	17.5–26.5	2.00	23.6	21.0–27.5	1.97
Head width**	24.7	20.0–30.0	2.24	27.7	22.9–36.5	3.57
Interorbital distance*	9.3	6.9–11.7	1.15	10.1	8.2–12.5	0.98
Eyelid width	4.6	3.4–5.6	0.55	4.8	3.4–6.6	0.70
Internarial distance*	3.9	3.0–5.2	0.47	4.3	3.0–5.9	0.69
Eye diameter**	6.1	5.0–7.6	0.68	6.6	5.7–7.8	0.55
Eye–nostril distance**	6.2	4.9–8.2	0.76	6.9	5.5–8.0	0.70
Orbit–jaw distance	3.3	2.3–4.4	0.53	3.5	2.6–5.1	0.73
Nostril–jaw distance**	4.2	3.2–5.7	0.59	4.8	4.0–5.8	0.54
Tympanum diameter**	3.2	2.0–4.6	0.55	3.8	2.9–4.9	0.56
Thumb length**	11.7	9.7–13.4	1.18	13.0	10.7–16.2	1.65
Third finger length**	21.3	18.4–25.7	1.72	23.6	19.9–28.6	2.78†
Disc width**	3.9	2.5–4.6	0.49	4.6	3.7–5.9	0.63

*Differences between the means of the sexes are significant (ANOVA, $P = 0.05$).

**Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

†Variances are non-homogeneous (Brown-Forsythe test, $P \leq 0.05$).

lates with the medial surface of the postorbital process of the maxilla via a long blunt-tipped process on the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located between the middle quadrants of the choanae.

Life History

The eggs hatch as froglets. Despite the relatively large number of specimens of this species, few reproductive data are available. One female (snout–vent length 75.2 mm) was brooding 26 embryos, with diameters of 7.2 mm each; another contained 33 embryos, 11.0 mm in diameter each, in the brood pouch. Yústiz (1978) noted that a female collected in the Parque Nacional Yacambu gave birth to three young on 27 June 1972; subsequently, 37 embryos were removed from the pouch. On 21 May 1973, 50 embryos (Stage 21) were removed from the pouch of another female from the same locality and placed in amphibian saline solution; 29 embryos died by 4 June, and the others died by 16 June.

Limited data suggest that the duration of the breeding season varies geographically. Males have been heard calling in January and April in Panama; December and February in Venezuela; and January, May, July, November, and December in Colombia. Brooding females were found in March, May, and November. Conceivably, *G. nicefori* breeds throughout the year across its range.

Advertisement Call

The call consists of a series of chicken-like "clucks." The first note is longest, and is followed by two to six (usually three) shorter notes. Duellman (1970) presented data on a recording made in Darién, Panama. Three call groups were emitted in a period of 8 seconds, followed by a 12-second interval and one more call group. The parameters are as follows: duration of primary note 0.5–0.6 seconds, duration of secondary notes 0.15–0.20 seconds, pulse rate 80–90 per second, fundamental frequency 87 Hz, and dominant frequency 957 Hz. The call of one individual sometimes seems to initiate a chorus that passes wave-like through a local population (e.g., up a mountain gully) (Myers and Duellman, 1982).

Distribution and Ecology

Gastrotheca nicefori has the widest geographical distribution in the genus (Fig. 11.19). It occurs from the Serranía de Tabasará (1600 m) in western Panama; and at elevations of 800–1600 m in the mountains (Serranía del Pirre, Serranía del Sapo, and Cerro Tacarcuna) in eastern Panama, southward through the Cordilleras Central (1480–2265 m) and Oriental (1140–1950 m) in

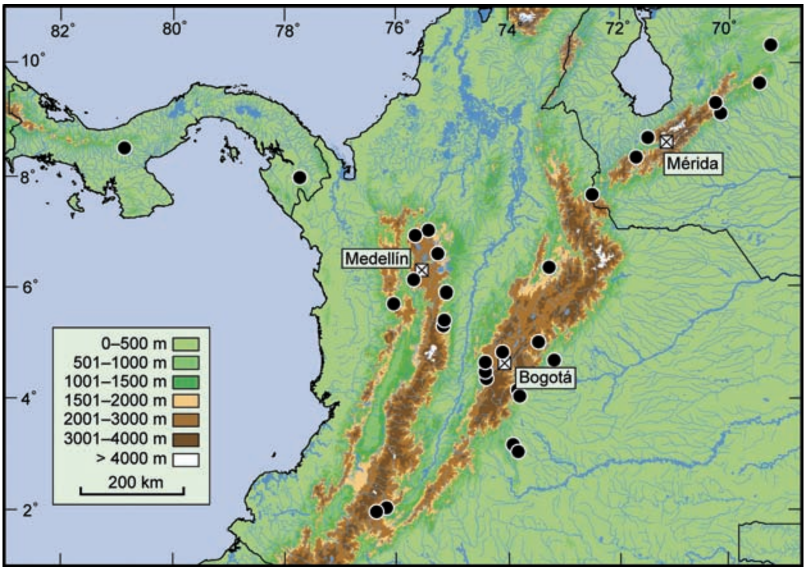

Fig. 11.19 Northwestern South America and Panama, showing the localities of known occurrences of *Gastrotheca nicefori*.

Colombia, and eastward on the northern slopes of the Mérida Andes (1330–2000 m) and southern slopes of the Serranía de Portuguesa (1700) in Venezuela. It also occurs at elevations of 400–1500 m in the isolated Serranía de la Macarena in eastern Colombia, and on the Pacific lowlands in Chocoan Colombia.

With the exception of specimens from El Carmen de Atrato in Chocoan Colombia and from the lower slopes of the Serranía de la Macarena in eastern Colombia, all individuals of *Gastrotheca nicefori* are from humid montane forest or cloud forest. These humid forests are discontinuous. Thus populations of *G. nicefori* in the various cordilleras and serranías are isolated from one another by drier and presumably uninhabitable environments at lower elevations.

Most individuals have been found at night to heights of 4 m above the ground, perched on branches of bushes and trees; one was in a rolled *Heliconia* leaf about 3 m above the ground; two were 2–3 m above the ground, calling from leaves of *Thalia*; and one was calling at night from a terrestrial bromeliad. Gutiérrez-Lamus et al. (2004) reported males, more than 10 m above the ground, calling from bromeliads. By day the frogs have been found in bromeliads, and one was sleeping on a bract of a small herb amid tangled vegetation at the edge of a stream.

Conservation Status

In the IUCN Red List, *Gastrotheca nicefori* is categorized as being of Least Concern, because of its wide distribution, tolerance of a degree of habitat modification, and presumed large population. Chytrid fungus infections have been reported for two specimens from two localities in the Mérida Andes in Venezuela (Lampo et al., 2008). These infected frogs were collected in 2004 and 2005.

Etymology

The specific name *nicefori* is a patronym for the late Hermano Nicéforo María, herpetologist and director of the Museo del Instituto de La Salle in Bogotá, Colombia.

Remarks

In juveniles the skin on the head is not co-ossified with the underlying dermal elements. The largest juvenile showing no co-ossification has a snout–vent length of 31.3 mm.

Duellman (1989) considered *Gastrotheca medemi*, *G. nicefori descampsi*, and *G. yacambuensis* to be junior synonyms of *G. nicefori*, but provided no evidence for his actions other than stating that there was no significant variation in morphometrics, structure, or coloration. Without any new data, Barrio-Amorós (1999) disagreed with Duellman's placement of *G. yacambuensis* in the synonymy of *G. nicefori*. Yet the synonymization of these taxa can be justified by numerous criteria.

Variation in morphometric data was analyzed using a stepwise discriminant function analysis on four samples: 6 individuals from the Serranía de la Macarena (type locality of *Gastrotheca medemi*), 6 from the southern part of the Cordillera Oriental in Colombia (nearest to the type locality of *G. nicefori descampsi*), 4 individuals from the Venezuelan Andes (type locality

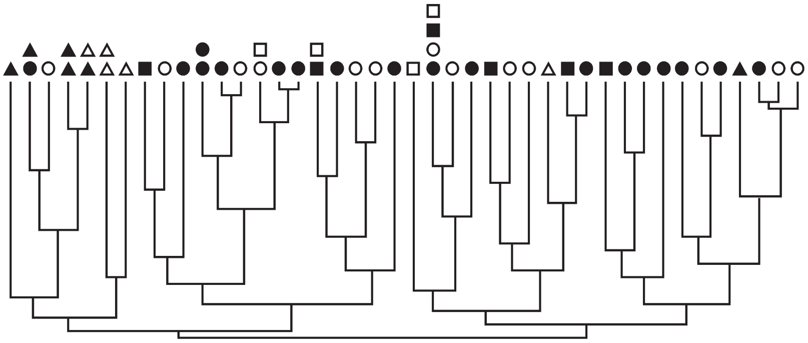

Fig. 11.20 Phenogram, based on a cluster analysis of characters of the color pattern in *Gastrotheca nicefori* in various parts of its range. Each symbol represents one individual. Solid circles = Cordillera Oriental in Colombia; open circles = Cordillera Central (except Departamento de Huila) in Colombia; solid squares = Panama; open squares = Venezuela (including the holotype of *G. yacambuensis*); solid triangles = Departamento de Huila in the southern part of the Cordillera Central in Colombia; open triangles = Serranía de Macarena in Colombia (including the holotype of *G. medemi*).

of *G. yacambuensis*), and 23 individuals from throughout the rest of the range of the species in Colombia and Panama. A jackknifed six-step model of $\log_{10}$ data revealed no discrimination of samples (Fig. 11.20). Separate and combined cluster analyses of structural characters and coloration showed that specimens from Venezuela clustered in three places with specimens from Colombia. Furthermore, five specimens from the Serranía de Macarena clustered together within those from Panama and those from other parts of Colombia, and one specimen clustered with a different group of individuals from Colombia. Of the six individuals from the southern part of the Cordillera Oriental in Colombia, four clustered together and two clustered independently, all within those from Panama and those from other parts of Colombia. Thus multivariate analyses of morphometric, structural, and color characters do not support the recognition of more than one taxon.

Cochran and Goin (1970:173) stated: "*Gastrotheca medemi* probably is most closely related to *G. nicefori*, from which it differs in its narrower head, shorter legs, and smaller tympanum." Lutz and Ruíz-C. (1977:14–15) based the description of *G. nicefori descampsi* on a single female and noted: "*G. n. descampsi* approaches *G. n. nicefori* by the concrescent skin of the head and other morphological details but diverges from it by the smaller size, the different color, the occipital border, and the rougher skin." The size differences alluded to in these descriptions are not valid (Table 11.10). The snout–vent lengths of the female holotypes of *G. medemi*, *G. nicefori*, and *G. nicefori descampsi* are at the lower range of variation (60.0–81.2 mm, $\bar{x} = 69.0$, $n = 16$) of females of the species. The proportions of the holotype of *G. medemi* fall within the range of variation of females of *G. nicefori*; percentages from the holotype of *G. medemi* are followed by the mean and then the range of 16 adult females of *G. nicefori*: tibia length/snout–vent length 45.9%, 51.7% (44.7%–54.6%); head width / <snout–vent length 37.2%, 40.1% (36.3%–43.1%); and eye diameter/tympanum diameter 52.5%, 57.8% (51.0%–62.3%). Because the holotype is lost, the other supposedly diagnostic characters of *G. nicefori descampsi* mentioned by Lutz and Ruíz-C. (1977) could not be checked. The granular appearance of the skin and dull "indigo" color may have resulted from preservation in strong formalin, as is apparent from the published photographs of the holotype (Lutz and Ruíz-C. 1977:13–14); the oblique appearance of the occipital ridge seems to be the result of distension of the skin on the back from large eggs in the anterior part of the pouch, as shown in the published photographs.

In his description of *Gastrotheca yacambuensis*, Yústiz (1978:88) stated: "En comparación con las *Gastrothecas* de Colombia que presentan co-osificación de la piel craneana: *G. cornutus* (Boulenger), *G. nicefori* Gaige y *G. medemi* Cochran-Goin, nuestra especie se separa por su cabeza tan larga como ancha y su vistosa coloración." My measurements of the holotype reveal a head length less than the head width (Table 11.10). The coloration is matched by many specimens of *G. nicefori* from Colombia.

Among the named populations of *Gastrotheca nicefori*, specimens from the Serranía de la Macarena are alike in having rather pale brown venters, with dark flecks on the throat and chest, and rather pale brown flanks with large creamy white spots, especially in the groin. In these features of coloration, they differ from

Table 11.10 Measurements of holotypes (all adult females) of four nominal species of *Gastrotheca*

Character	*G. nicefori* UMMZ 73242	*G. medemi* UMMZ 123068	*G. n. descampsi* ICN 318*	*G. yacambuensis* MBUCV 6051
Snout–vent length	61.0	61.6	61.0	78.4
Tibia length	34.2	28.2	31.0	39.2
Foot length	31.0	28.7	36.0	37.0
Head length	22.7	21.1	21.0	27.3
Head width	25.3	22.9	25.0	32.8
Interorbital distance	9.6	8.2	9.0	12.0
Eyelid width	4.6	4.3	—	5.0
Internarial distance	3.6	3.9	5.0	4.8
Eye diameter	6.6	6.1	6.0	7.3
Eye–nostril distance	6.8	7.2	5.0	7.5
Orbit–jaw distance	3.0	3.1	—	4.6
Nostril–jaw distance	4.0	4.2	—	4.5
Tympanum diameter	3.7	3.2	2.5	4.8
Thumb length	12.0	10.7	—	15.5
Third finger length	22.2	21.3	—	28.2
Disc width	4.2	4.3	—	5.1

*Specimen lost; data are from the type description (Lutz and Ruíz-C., 1977).

most other specimens, none of which has equally large spots on the flanks and flecks on the venter.

The inclusion of four nominal taxa in *Gastrotheca nicefori* is based on morphological data on preserved specimens and notes on living specimens from selected parts of its range. The isolation of populations of *G. nicefori* on separate mountain ranges in Panama, Colombia, and Venezuela invites molecular comparisons of these populations. If such future studies reveal major differences, *G. medemi* is the name available for the population in the Serranía de la Macarena, and *G. yacambuensis* for the population in the Venezuelan Andes.

Gastrotheca (*Duellmania*) *orophylax* Duellman and Pyles

Gastrotheca orophylax Duellman and Pyles, 1980:5.—Holotype: KU 164243 from 11 km [by road] ESE of Papallacta, 2660 m, Provincia de Napo, Ecuador.

Gastrotheca (*Opisthodelphys*) *orophylax*—Dubois, 1987:32.

Diagnosis

Adults of this moderately large species attain a maximum snout–vent length of 74.0 mm. The tibia length is less than 55% of the snout–vent length, and is barely longer than the foot. The interorbital distance is about twice the width of the upper eyelid. The skin on the dorsum is smooth or areolate, not co-ossified with the skull (co-ossified with the frontoparietals in large females), and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is granular. The first finger is shorter than the second. The discs on the fingers are much wider than the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and a point midway between the penultimate and distal subarticular tubercles on the fifth toe. The dorsum is uniformly green. Markings on the head consist solely of a narrow pale labial stripe. A pale dorsolateral stripe is absent. The flanks are uniformly green; the venter is pale green.

Gastrotheca orophylax is like *G. carinaceps* in being a uniformly green frog, except that *G. orophylax* has a narrow bronze labial stripe, short bronze supratympanic stripe, and bronze tympanum (stripes absent and tympanum green in *G. carinaceps*). *G. carinaceps* also differs by having the first and second fingers equal in length, and by having an inclined (instead of truncate) snout in profile. In size and structure *G. orophylax* is like *G. monticola* and *G. plumbea*, both of which commonly have pale dorsolateral, labial, and supracloacal stripes. Furthermore, most specimens of *G. monticola* have dark markings dorsally and black spots ventrally, and *G. plumbea* has dark brown flanks. *G. longipes* also is uniformly green (or nearly so), but it differs from *G. orophylax* in having an inclined (instead of truncate) snout in profile, narrower interorbital distance that is about 125% of the width of the upper eyelid, first and second fingers equal in length, and a green tympanum. Superficially, unicolored individuals of *G. aureomaculata* are similar to *G. orophylax*, but the former differs by having dorsal skin that is more coarsely areolate, less webbing on the feet, and a distinctive golden tympanum.

Description

The following description is based on 56 specimens. The body is moderately robust; the maximum snout–vent length is 59.1 mm in males, and 74.0 mm in females (but see "Remarks"). The head is slightly wider than long, and nearly as wide as the body. The snout is bluntly rounded in dorsal view, and is truncate in profile. The canthus rostralis is weakly angular in cross-section. The loreal region is barely concave; the lips are rounded. The top of the head is flat. The interorbital distance is about twice the width of the upper eyelid. The internarial area is flat. The nostrils are barely protuberant, and are directed anterolaterally at the level of the anterior margin of the lower jaw. The diameter of the eye is slightly less than its distance from the nostril. The tympanum is vertically elliptical, and is separated from the eye by a distance about twice the length of the tympanum. The tympanic annulus is indistinct and tubercular. The supratympanic fold is moderately weak, and extends from the posterior corner of the orbit to the flank.

The arm is moderately robust, and lacks ulnar tubercles. The hand is moderate in size. The fingers are long, and bear large elliptical discs; the width of the disc on the third finger is half again the width of the tympanum. The relative lengths of the fingers are I < II < IV < III. The fingers are unwebbed. The subarticular tubercles are moderately large and round; none are bifid. The supernumerary tubercles are moderately small, subconical, and present only on the proximal segments. The palmar tubercle is low and bifid; the prepollical tubercle is elliptical; the thumb bears nuptial excrescences in breeding males. The hind limb is moderately robust. The tibia length is about 49% of the snout–vent length; the foot length is about 47% of the snout–vent length. A calcar and tarsal tubercles are absent. The inner tarsal fold is weak, and extends the full length of the tarsus. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is flat, ovoid, and barely visible from above. The toes are long. The relative lengths of the toes are I < II < III < V < IV. The toes are about one-half webbed; the webbing formula is **I**2—2^{+}**II**2^{-}—3**III**2—(3^{-}–3)**IV**(3–3^{+})—(1½–2)**V**. The subarticular tubercles are moderately small and round. The supernumerary tubercles are small, subconical, and present only proximally.

The skin on the dorsum of the head, body, and limbs is smooth (68%) or areolate (32%); it is co-ossified with the underlying bones on the top of the head in some large females (see "Remarks"). The skin on the flanks is areolate; the skin on the throat, belly, and ventral surfaces of the thighs is granular. Cloacal tubercles and folds are absent. The opening of the brood pouch is U-shaped, with the anterior border at the level of the posterior edge of the sacrum. The dentigerous processes of the vomers are narrowly separated medially, at the level of the posterior margins of the small round choanae. Each process bears six to eight teeth.

COLOR IN PRESERVATIVE

The dorsum is uniformly dark bluish gray; the venter is dull gray.

COLOR IN LIFE

This is a predominately green frog, with a bronze iris reticulated with black (Fig. 11.21). The following are descriptions of colors in living individuals from two localities.

Two individuals (KU 164243–44) from 11 km ESE Papallacta, Provincia de Napo, Ecuador.—The dorsum is emerald green, with a bronze supratympanic stripe and a greenish-yellow labial stripe. The flanks are green. There is a bronze suffusion on the outer edges of the forearms and feet, in the cloacal region, and on the toes. The axilla, groin, and distal part of the thigh are pale blue. The palmar and plantar surfaces are dark gray. The ventral surfaces of the thighs are grayish bronze; the other ventral surfaces are green (W. E. Duellman field notes, 22 March 1975).

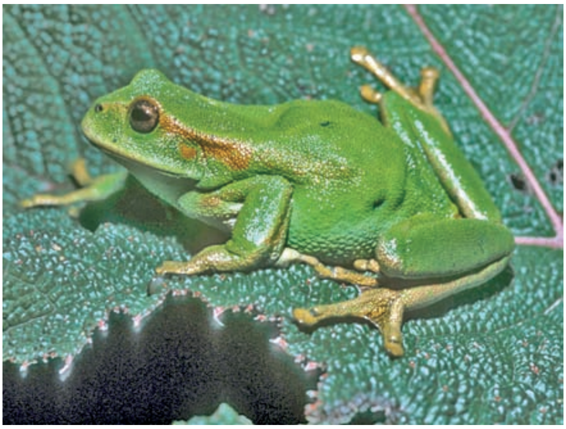

Fig. 11.21 *Gastrotheca orophylax* (KU 164243, holotype), female, 70.1 mm SVL, 11 km ESE Papallacta, 2660 m, Napo, Ecuador. Photo by W. E. Duellman.

A series (KU 178570–79) from 5.7 km NW El Carmelo, Provincia de Carchi, Ecuador.—The dorsum is dark green, with a brown postocular stripe extending to the shoulder; the toe pads are darker green. The lower flanks and hidden surfaces of the limbs have a pale blue wash on the green; the undersides of the limbs and feet are brown black; the belly and vocal sac are blue green (J. D. Lynch field notes, 21 July 1977).

MEASUREMENTS

Although females are larger than males, the differences between the means of many of the measurements are not significant (Table 11.11).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a heterogeneous fine pit-and-ridge pattern. The nasals articulate medially, and are fused to one another and the sphenethmoid posteriorly; posterolaterally, the nasals articulate at the anterolateral margin of the frontoparietals. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange and a small otic flange. The temporal arcade is complete. The frontoparietal covers only the anterior epiotic eminence, and is partially fused to it; hence the carotid canal is only partly closed, and exits the skull posteriorly adjacent to the posterior epiotic

Table 11.11 Univariate statistics for adults of *Gastrotheca orophylax* and *G. plumbea*

		G. orophylax (24 males, 24 females)			*G. plumbea* (5 males, 3 females)		
Character	Sex	Mean	Range	SD	Mean	Range	SD
Snout–vent length	males	53.7*	47.6–59.1	3.25**	56.7*	42.1–61.0	3.77
	females	59.3*	50.8–74.0	5.94**	64.2*	58.2–73.0	4.24
Tibia length	males	26.3*	21.7–29.5	1.64**	28.3*	22.6–32.3	1.92
	females	29.8*	25.0–37.0	3.40**	32.4*	30.2–34.5	1.42
Foot length	males	25.5*	22.0–27.6	1.69**	27.2*	21.0–30.6	1.89
	females	28.5*	24.1–36.9	3.40**	31.6*	28.1–37.0	2.10
Head length	males	18.2*	15.2–20.2	0.70	18.8*	16.1–21.2	0.40
	females	19.9*	17.5–23.8	0.95	21.5*	19.4–25.2	1.23
Head width	males	20.7	18.0–22.5	1.19	20.8*	17.4–23.2	1.12
	females	22.6	19.8–28.0	2.30	23.6*	21.6–26.9	1.44
Interorbital distance	males	6.9*	6.0–7.5	0.42	6.8*	5.4–7.5	0.45
	females	7.6*	6.3–10.4	1.01	7.9*	7.1–8.7	0.53
Eyelid width	males	3.6	2.8–4.7	0.61	3.8*	3.0–4.6	0.43
	females	3.6	2.4–3.7	0.60**	4.1*	3.3–5.2	0.50
Internarial distance	males	3.4	2.9–4.1	0.27	3.4*	2.8–4.0	0.43
	females	3.7	3.1–4.8	0.48	4.0*	3.2–5.0	0.52
Eye diameter	males	4.6	3.9–5.6	0.23	4.3*	3.1–5.0	0.44
	females	5.0	4.3–6.4	0.48	5.2*	4.5–6.9	0.60
Eye–nostril distance	males	5.4	4.9–5.9	0.27	5.6*	4.8–6.5	0.37
	females	5.8	5.1–7.5	0.63	6.2*	5.5–6.8	0.43
Orbit–jaw distance	males	3.1	2.4–3.6	0.27	3.0*	2.3–3.6	0.34
	females	3.4	1.6–4.5	0.51	3.6*	2.7–4.4	0.51
Nostril–jaw distance	males	4.1	2.9–4.7	0.38	4.3*	3.2–4.9	0.38
	females	4.5	3.4–5.9	0.39	5.0*	4.1–6.5	0.60
Tympanum diameter	males	2.6	1.8–4.7	0.37	2.7	1.9–4.4	0.53
	females	2.8	2.2–4.0	0.43	3.0	2.3–4.4	0.54
Thumb length	males	10.1	8.3–12.5	0.85	10.7*	8.2–12.6	0.85
	females	11.0	8.8–14.0	1.55**	12.6*	11.3–15.0	1.02
Third finger length	males	18.6	15.8–21.7	1.49**	19.9*	15.7–21.9	1.23
	females	20.6	17.7–25.8	2.46**	22.7*	20.3–26.0	1.67
Disc width	males	2.9	2.4–3.6	0.32**	3.5	2.5–3.9	0.28
	females	3.3	2.5–4.4	0.50**	4.0	3.1–5.0	0.48

*Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

**Differences between the means of the two species are significant (ANOVA, $P \leq 0.01$).

eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for about half the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The postorbital process of the maxilla is large, and has a horizontal articulation with the wide zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the otic plate articulates with and narrowly overlaps the crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in length, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified posterior to the midlength of the orbit, but is not synostosed with the prootic. The neopalatines are widely separated medially; each bears an irregular ridge ventrally. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a long acuminate recurved process on the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located between the middle quadrants of the choanae.

Life History

The eggs of *Gastrotheca orophylax* undergo direct development into froglets in the brood pouch. Twelve brooding females having snout–vent lengths of 50.8–74.0 mm ($\bar{x} = 59.4$), collected in March, May, June, and July, contained 15–37 ovarian eggs ($\bar{x} = 22.3$), of which the diameters of the ova or embryos were 5.2–7.5 mm ($\bar{x} = 6.1$). Del Pino and Escobar (1981) reported four females having an average snout–vent length of 60.0 mm brooding an average of 28 eggs with diameters of 5.0 mm. Two brooding females collected on 21 July at El Carmelo, Provincia de Carchi, Ecuador, gave birth to young on 31 August and 25 September. Ten of these young have snout–vent lengths of 15.7–17.2 mm ($\bar{x} = 16.1$).

Del Pino and Escobar also noted that parturition in the laboratory took place in water, and that developing embryos are tadpole-like, with pigmentation and well-developed mouthparts and tails. The authors removed embryos from the pouch and raised the non-feeding larvae in water to metamorphosis; they estimated that the duration of incubation is 88 days.

Advertisement Call

The call usually consists of a single short note, with a dominant frequency at 990 Hz, but there may be a series of up to five notes (Sinsch and Juraske, 2006; Fig. 6.8C).

Distribution and Ecology

This species is known from elevations of 2620–3074 m in the cloud forest and subpáramo on the Amazonian slopes of the Cordillera Oriental of the Andes in northern Ecuador and extreme southern Colombia (Fig. 11.22). One individual was under a stone by day; all others were up to 2 m above the ground on vegetation at night; nearly all specimens observed in Ecuador

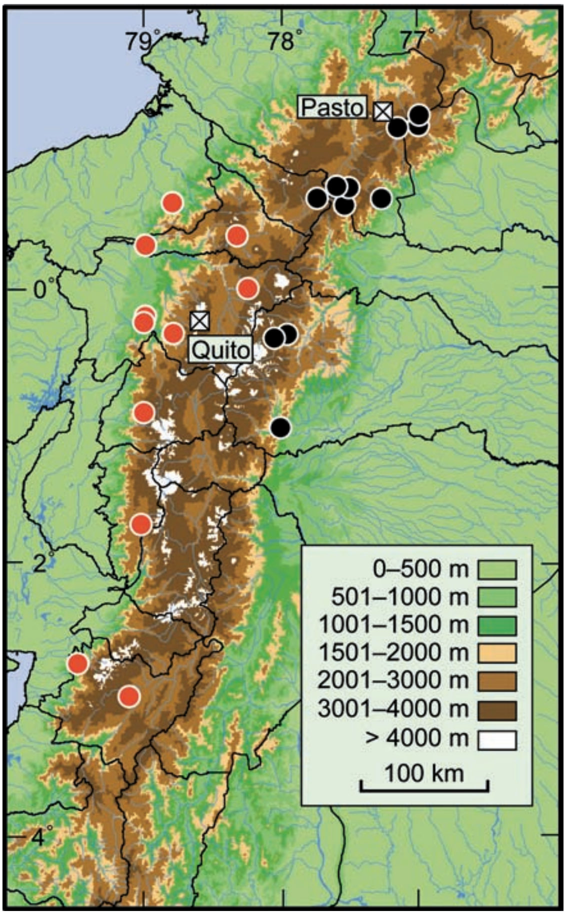

Fig. 11.22 Andean region of Ecuador and southern Colombia, showing the localities of known occurrences of *Gastrotheca orophylax* (black) and *G. plumbea* (red).

were perched on the large leaves of the herb *Gunnera* (Haloragaceae).

Conservation Status

Gastrotheca orophylax is categorized as Endangered in the IUCN Red List, because of habitat destruction within its limited geographic range.

Etymology

The specific name is derived from the Greek *oros*, meaning "mountain," and the Greek *phylax*, meaning "guard" or "watchman." Duellman and Pyles (1983) used the name in allusion to these frogs probably witnessing a band of Spanish Conquistadores that passed by the type locality on their way to the Amazon in 1539.

Remarks

Two brooding females (NMG 1099–1100) from Río Mulatos, Provincia de Napo, Ecuador (the southernmost known locality for the species) are much larger than specimens from farther north. These two specimens have snout–vent lengths of 83.5 and 88.7 mm. Although they are like other individuals of *Gastrotheca orophylax* in coloration and webbing, they differ by having dorsal skin that is more granular and extensive cranial-dermal co-ossification involving the nasals, frontoparietals, cristae paroticae, and squamosals. These two individuals seem to represent a developmental extreme in the species; as noted in several species of *Gastrotheca* (e.g., *G. testudinea* and *G. trachyceps*), co-ossification of the skin with dermal cranial elements is an ontogenetic phenomenon.

Gastrotheca orophylax is like *G. plumbea* in that when individuals are disturbed, they exude a pale blue slime (see "Remarks" under *G. plumbea*); but a multivariate analysis of their morphometrics, structural features, and coloration showed distinctive differences between *G. orophylax* and *G. plumbea* (Duellman and Pyles, 1980). Both sexes of *G. orophylax* are significantly smaller than those of *G. plumbea* in snout–vent length, tibia length, foot length, third finger length, and disc width, whereas only females are smaller in eyelid width and thumb length (Table 11.11).

Gastrotheca (*Duellmania*) *plumbea* (Boulenger)

Nototrema plumbeum Boulenger, 1882:417.—Holotype: BMNH 1947.2.31.19 from Intag, Provincia de Imbabura, Ecuador.

Gastrotheca plumbeum—Peters, 1955:346.

Gastrotheca (*Opisthodelphys*) *plumbea*—Dubois, 1987:32.

Diagnosis

This moderately large species attains a maximum snout–vent length of 73.0 mm. The tibia length is less than 50% of the snout–vent length, and is slightly longer than the foot. The interorbital distance is about twice the width of the upper eyelid. The skin on the dorsum is smooth to weakly areolate, not co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is granular anteriorly and ventrally, and smooth posteriorly. The first finger is shorter than the second. The discs on the fingers are much wider than the digits. The fingers are unwebbed; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and a point midway between the penultimate and distal subarticular tubercles on the fifth toe. The dorsum is uniformly green. Markings on the head consist solely of a pale labial stripe. A pale dorsolateral stripe is present. The flanks are uniformly brown; the venter is creamy tan.

Gastrotheca plumbea has a pattern like that in some specimens of *G. pseustes*, but it differs from that species by having the first finger shorter than the second, and by having larger digital discs. The presence of pale labial and dorsolateral stripes separates *G. plumbea* from *G. orophylax* and unicolored individuals of *G. aureomaculata*, and the uniformly pale venter distinguishes it from *G. monticola*, which usually has a spotted venter. The absence of black and blue mottling in the groin and on the hidden surfaces of the thighs distinguishes *G. plumbea* from *G. argenteovirens* and *G. trachyceps*.

Description

The following description is based on 50 specimens. The body is moderately robust; the maximum snout–vent length is 61.0 mm in males, and 73.0 mm in females. The head is slightly wider than long, and nearly as wide as the body. The snout is bluntly rounded in dorsal view, and in profile is steeply inclined from the nostrils to its tip. The canthus rostralis is rounded in cross-section. The loreal region is barely concave; the lips are rounded. The top of the head is flat. The interorbital distance is slightly less than or equal to the width of the upper eyelid. The internarial area is flat. The nostrils are barely protuberant, and are directed anterolaterally below the terminus of the canthus rostralis at the level of the anterior margin of the lower jaw. The diameter of the eye is slightly larger than its distance from the nostril. The tympanum is vertically ovoid, and is separated from the eye by a distance at least half again the diameter of the tympanum. The tympanic annulus is distinct and smooth posteriorly, but indistinct and tubercular anteriorly and ventrally. The supratympanic fold is moderately heavy, and extends from the posterior corner of the orbit to a point above the insertion of the arm.

The arm is moderately robust, and lacks ulnar tubercles. The hand is moderate in size. The fingers are long, and bear large round discs; the width of the disc on the third finger is greater than the length of the tympanum. The relative lengths of the fingers are I < II < IV < III. The fingers are unwebbed. The subarticular tubercles are large and round; none are bifid. The supernumerary tubercles are small, round, and present on the proximal segments of the fingers. The palmar tubercle is low and bifid; the prepollical tubercle is elongately elliptical; the thumb bears nuptial excrescences in breeding males. The hind limb is robust. The tibia length is about 49% of the snout–vent length; the foot length is about 48% of the snout–vent length. A calcar and tarsal tubercles are absent. The inner tarsal fold is weak, and extends the full length of the tarsus. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is flat, ovoid, and barely visible from above. The toes are long. The relative lengths of the toes are I < II < III < V < IV. The toes are about one-half webbed; the webbing formula is **I**2—2**II**2^{-}—3**III**2—3**IV**3—(1½–2)**V**. The subarticular tubercles are small and round; the supernumerary tubercles are minute, and are present only on the proximal segments of the toes.

The skin on the dorsal surfaces of the head, body, and limbs is smooth (64%) or areolate (36%). The skin on the flanks is areolate; the skin on the throat, belly, and ventral surfaces of the thighs is granular. Cloacal tubercles are absent, but a broad vertical fold exists on either side of the cloacal opening. The opening of the brood pouch is U-shaped, with the anterior border at the level of the posterior edge of the sacrum. The dentigerous processes of the vomers are posteromedially inclined, and are narrowly separated medially between the small round choanae. Each process bears seven to nine teeth.

COLOR IN PRESERVATIVE

The dorsum is uniformly gray; the flanks are brown, usually (94%) separated from the dorsal coloration by a pale dorsolateral stripe. A pale labial stripe is present; a dark canthal stripe is absent. A pale supracloacal stripe usually (65%) is absent; a dark patch in the cloacal region usually (82%) is absent. The venter and hidden surfaces of the thighs are uniformly creamy tan.

COLOR IN LIFE

Most individuals have a green dorsum, with a prominent pale dorsolateral stripe (Fig. 11.23). The iris has been described as pale olive to pale green in specimens from Provincia de Cotopaxi, and dull bronze with black reticulations in specimens from Provincia de Pichincha. The following are descriptions of living individuals.

KU 164232 from 5 km ESE Chiriboga, Provincia de Pichincha, Ecuador.—The dorsum is emerald green. The flanks and hidden surfaces of the limbs are dark brown, with bronze flecks. The labial, dorsolateral, tarsal, and supracloacal stripes are bronze. The venter is bronze brown; the axilla and groin are suffused with dull blue (W. E. Duellman field notes, 11 May 1975).

KU 164229–31 from 9.5 km NW Nono, Provincia de Pichincha, Ecuador.—The dorsum is bright green, with

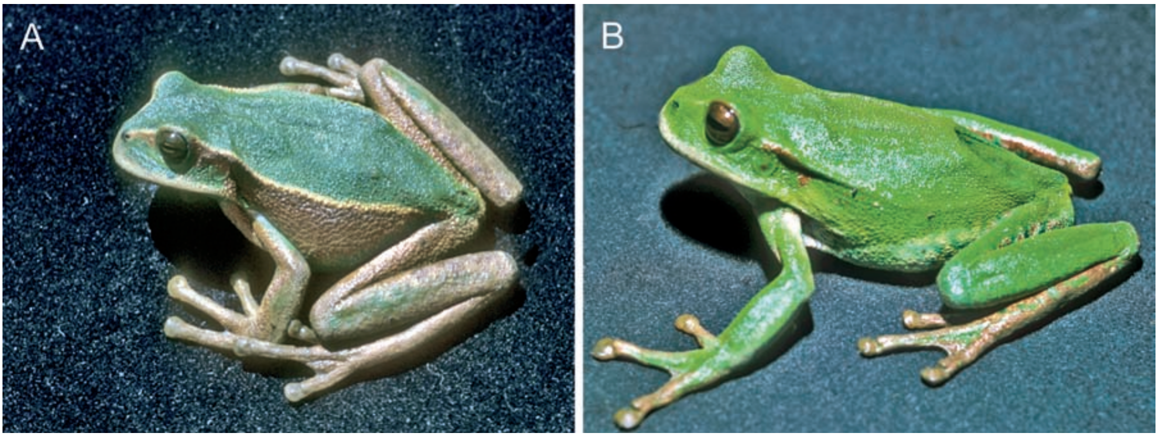

Fig. 11.23 *Gastrotheca plumbea*. A: KU 142614, male, 54.1 mm SVL, Pilaló, 2320 m, Cotopaxi, Ecuador. B: KU 164229, female, 62.6 mm SVL, 9.5 km NW Nono, 2530 m, Pichincha, Ecuador. Photos by W. E. Duellman.

or without yellow flecks. The labial stripe is creamy white; the supratympanic bar is dark bronze. The groin and hidden surfaces of the hind limbs are pale blue at night, and by day are bronze tan with dark blue or bluish-green spots. At night the venter is cream. By day the throat is pale green; the belly is dull greenish yellow, yellowish tan, or dull brown (W. E. Duellman field notes, 11 April 1975).

KU 178501–26 from Pilaló, Provincia de Cotopaxi, Ecuador.—The dorsum is brown, with golden dorsolateral and labial stripes in most males; the flanks are darker brown, with some green and yellow on the lower flanks. Some males are green; others are brown, with green patches. The hands, feet, and tarsi are brown, even if the remainder of the frog is green. The throat is yellowish brown; the rest of the venter is dirty bronze yellow. Females are green, with yellow dorsolateral and labial stripes; large females have yellow spots on the dorsum. The inner edges of the digits and tarsi are brown. The chin is pale green; the venter has a yellowish-brown wash. Some females have brown on the anterior flanks. The axilla and groin are dull blue in all individuals (J. D. Lynch field notes, 29 June 1977).

MEASUREMENTS

The means of all measurements, except tympanum diameter and the width of the disc on the third finger, are significantly larger in females than in males (Table 11.11).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous semicoarse pit-and-ridge pattern. The nasals neither articulate with one another medially, nor are fused to the sphenethmoid posteriorly; posterolaterally, the nasals articulate at the anterolateral margin of the frontoparietals. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange and a moderate-sized otic flange. The temporal arcade is not complete. The frontoparietal covers the anterior epiotic eminence and part of the posterior epiotic eminence. The frontoparietal is partially fused to the epiotic eminences; hence the carotid canal is only partly closed, and exits the skull posteriorly adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 31° and 45°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for about half the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The postorbital process of the maxilla is large, and has a horizontal articulation with the wide zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the otic plate articulates with and narrowly overlaps the crista parotica. The dorsal part of the stapedial footplate is two to three times larger than the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are widely separated medially; each bears an irregular ridge ventrally. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a long acuminate recurved process on the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located between the middle quadrants of the choanae.

Life History

The eggs of *Gastrotheca plumbea* undergo complete development in the pouch and hatch as froglets. Two females with snout–vent lengths of 60.3 and 62.9 mm were brooding 14 and 34 eggs having diameters of 4.5 and 5.9 mm, respectively. Del Pino and Escobar (1981) reported three females (mean snout–vent length of 69 mm) with an average of 28 eggs, each 4 mm in diameter, in their pouches. Auber-Thomay et al. (1990) reported females brooding 20–28 eggs, each 6.8 mm in diameter. According to del Pino and Escobar (1981), the embryos of *G. plumbea*, like those of *G. orophylax* but unlike those of other direct-developing species studied, develop through stages typical of tadpoles: with pigmentation, and with well-developed mouthparts and tails. Furthermore, these authors removed embryos from the pouch and raised them in water until the nonfeeding tadpoles metamorphosed.

Males have been heard calling in April, June, and July. Calling males are abundant at Pilaló, Provincia de Cotopaxi, Ecuador, in June and July; several males were observed there in March, but none was calling. Brooding females have been found in June and July at Pilalo. One of these females gave birth in Quito on 30 September; del Pino and Escobar (1981) estimated that the duration of incubation is 85–118 days, and they noted that during parturition the female uses her hind limbs to disgorge the young from the pouch. Another female gave birth to 26 young on 7 December 2013 (L. Coloma, pers. comm.).

Advertisement Call

The call consists of a single short note, with a dominant frequency of 970 Hz (Sinsch and Juraske, 2006).

Distribution and Ecology

This species is restricted to cloud forest at elevations of 1300 to 3070 m on the Pacific slopes of the Cordillera Occidental in Ecuador (Fig. 11.22). Throughout the year, adults have been found by day in bromeliads. In May one individual was perched on a boulder in a stream by day. At night some individuals have been found on branches of bushes in ravines, but most are perched on large hirsute leaves of the herb *Gunnera* (Haloragaceae). Juveniles were reported from the sheaths of bananas (Auber-Thomay et al., 1990).

Conservation Status

In the IUCN Red List, this species is listed as Vulnerable because of its fragmented range, within which habitat destruction is evident.

Etymology

The specific name is derived from the Latin *plumbeus*, meaning "of lead." Boulenger (1882) apparently applied the name because of the gray color of the preserved holotype.

Remarks

Duellman and Pyles (1980) provided a multivariate analysis showing distinctive differences between *Gastrotheca plumbea* and *G. orophylax*. Differences in morphometrics are evident from univariate statistics (Table 11.11). In a phylogenetic tree generated from molecular data, *G. orophylax* and *G. plumbea* are sister species (Wiens et al., 2007; Blackburn and Duellman, 2013; chapter 3).

When disturbed, these frogs exude an aromatic pale blue slime. Skins of three specimens were sent to the late Dr. Vittorio Erspamer (Department of Biochemistry, Universiti Roma) for an analysis of skin peptides and amines. These skins lacked active substances and were essentially the same as the skins of *Gastrotheca pseustes* and *G. riobambae* (V. Erspamer, pers. comm.). The latter species do not exude an aromatic slime.

Gastrotheca (*Duellmania*) *riobambae* (Fowler)

Hyla riobambae Fowler, 1913:157.—Holotype: ANSP 16161 from Riobamba, Provincia de Chimborazo, Ecuador.

Hyla quitoe Fowler, 1913:159.—Holotype: ANSP 18235 from Quito, Provincia de Pichincha, Ecuador. Synonymy fide Duellman and Fritts, 1972:11.

Chorophilus olivaceus Andersson, 1945:85.—Holotype: NHRM 1965 from "Río Napo, 400 m" [? = Baños, Provincia Tungurahua, Ecuador]. Synonymy fide Duellman and Fritts, 1972:11.

Gastrotheca marsupiata ecuatoriensis Vellard, 1957:43 (nomen nudum). Synonymy fide Duellman and Fritts, 1972:11.

Gastrotheca riobambae—Duellman and Fritts, 1972:11; Duellman and Hillis, 1987:163.

Gastrotheca cavia Duellman, 1974:5.—Holotype: KU 148532 from Isla Pequeña, Lago Cuicocha, 2890 m, Provincia de Imbabura, Ecuador. Synonymy fide Duellman and Hillis, 1987:163.

Gastrotheca (*Duellmania*) *riobambae*—Dubois, 1987:33.

Diagnosis

This medium-sized species attains a maximum snout–vent length of 66.4 mm. The tibia length is less than 45% of the snout–vent length, and is slightly shorter than the foot. The interorbital distance is slightly wider than the width of the upper eyelid. The skin on the dorsum is smooth, areolate, or granular. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first and second fingers are equal in length. The discs on the fingers are slightly wider than the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends maximally to the penultimate subarticular tubercle on the fourth and fifth toes. The dorsum is green or brown, usually with darker broad paravertebral marks. Markings on the head consist of a pale labial stripe and, in some specimens, a dark canthal stripe. A pale dorsolateral stripe usually is not present. The flanks pale are gray or tan, with dark spots; the venter is cream, with dark spots.

Gastrotheca riobambae is like *G. espeletia* and *G. pseustes* in having short limbs and small digital discs. It differs from both in having more extensive webbing on the feet, and by having bold dark spots or mottling on the ventral surfaces of the shank. Furthermore, the snout is more rounded in *G. riobambae* than in *G. pseustes*, and less protruding than in *G. espeletia*.

Description

The following description is based on 209 specimens. The body is robust. The maximum snout–vent length is

56.8 mm in males, and 66.4 mm in females. The head is slightly wider than long. The snout is rounded in dorsal view, and is acutely rounded and protrudes beyond the jaw in profile. The canthus rostralis is slightly curved, and angular in cross-section. The loreal region is slightly concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 110% of the width of the upper eyelid. The internarial area is flat. The nostrils are not protuberant, and are directed anterolaterally at the terminus of the canthus rostralis at a level posterior to the anterior margin of the lower jaw. The diameter of the eye is slightly greater than its distance from the nostril. The tympanum is nearly round, slightly higher than long, and separated from the eye by a distance slightly greater than the length of the tympanum. The tympanic annulus is distinct and smooth. The moderately heavy supratympanic fold extends from the posterior corner of the orbit to a point above the insertion of the arm, and obscures the upper edge of the tympanum.

The arm is moderately robust. The hand is medium sized. The fingers are moderately long, and are unwebbed. The discs on the fingers are small, slightly wider than the digits; the width of the disc on the third finger is slightly less than the length of the tympanum. The relative lengths of the fingers are I = II < IV < III. The subarticular tubercles are moderately large and subconical; none are bifid. The supernumerary tubercles are small, subconical, and numerous on the proximal segments of the digits. The palmar tubercle is low and weakly bifid; the prepollical tubercle is elongately elliptical; in breeding males the thumb bears a tan nuptial excrescence. The hind limb is moderately short and robust. The tibia length is 40.2%–42.9% ($\bar{x}$ = 41.5) of the snout–vent length; the foot length is 42.3%–48.5% ($\bar{x}$ = 44.8) of the snout–vent length. A calcar is absent. The inner tarsal fold is weak, and is barely evident on the distal one-fourth of the tarsus. The outer metatarsal tubercle is small, low, and round; the inner metatarsal tubercle is elevated, elliptical, and visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III = V < IV. Webbing is absent between Toes I, II, and III. The outer toes are about one-third webbed; the webbing formula is **IV**(2–3)—(2–2½)**V**. The subarticular tubercles are moderately small and subconical; the supernumerary tubercles are small, round, and present only on the basal segments of the digits.

The texture of the skin on the dorsum of the head, body, and limbs is variable, either smooth (45%), areolate (50%), or granular (5%). The skin on the flanks is areolate; the skin on the belly and ventral surfaces of the thighs is granular. Tubercles are absent on the upper eyelids. Cloacal folds and tubercles are absent. The opening of the brood pouch is narrowly U-shaped, with the anterior edge of the opening just posterior to the level of the sacrum. The dentigerous processes of the vomers are short, nearly transverse, and well-separated medially at a level just posterior to the small round choanae. Each process bears three to five teeth.

COLOR IN PRESERVATIVE

The dorsum is tan or dull bluish gray, either unmarked (19%), or with dark brown or green continuous or fragmented paravertebral marks (81%). A pale labial stripe usually (88%) is absent. A dark canthal stripe usually (88%) is present. A pale dorsolateral stripe usually (73%) is absent; a pale supracloacal stripe usually (62%) is present. The dorsal surfaces of the shanks usually (97%) have dark spots. The flanks are pale with dark spots (98%) or uniformly dark (2%). The anterior surfaces of the thighs are pale tan or bluish tan, with dark mottling; the posterior surfaces of the thighs are uniformly pale (37%) or pale with dark spots (63%). The throat, chest, and belly are uniformly cream (3%) or cream with dark flecks, spots, or mottling (87%). The vocal sac is gray; the ventral surfaces of the shanks are cream, with distinct dark spots or mottling.

COLOR IN LIFE

The dorsum is tan or various shades of green, with or without darker brown or green markings (Fig. 11.24). Considerable variation obtains not only in the dorsal coloration, but also in that of the flanks, hidden surfaces of the thighs, and venter, as illustrated by the following descriptions of colors in living individuals from throughout Ecuador.

KU 111613–25 from Quito, Provincia de Pichincha.—The dorsum is green or brown, with or without olive spots or stripes. A brown to black lateral band, beginning at the nostril, is bordered above by a white stripe. The posterior surfaces of the thighs are pale green or pale brown, with creamy white spots. The venter is yellow to cream, with or without brown spots (J. D. Lynch field notes, 12 July 1967).

KU 120725–31 from 15 km E Riobamba, Provincia de Chimborazo.—The dorsum is pale brown, with brown spots or stripes with darker edges. One individual has a green middorsal blotch, and another has green stripes edged with black. The flanks are paler than the dorsum, and have brown spots. The axilla, groin, and posterior surfaces of the thighs are green; the venter is yellowish cream, with brown reticulations (J. D. Lynch field notes, 21 June 1968).

KU 120733–40 from Ambato, Provincia de Tungu-

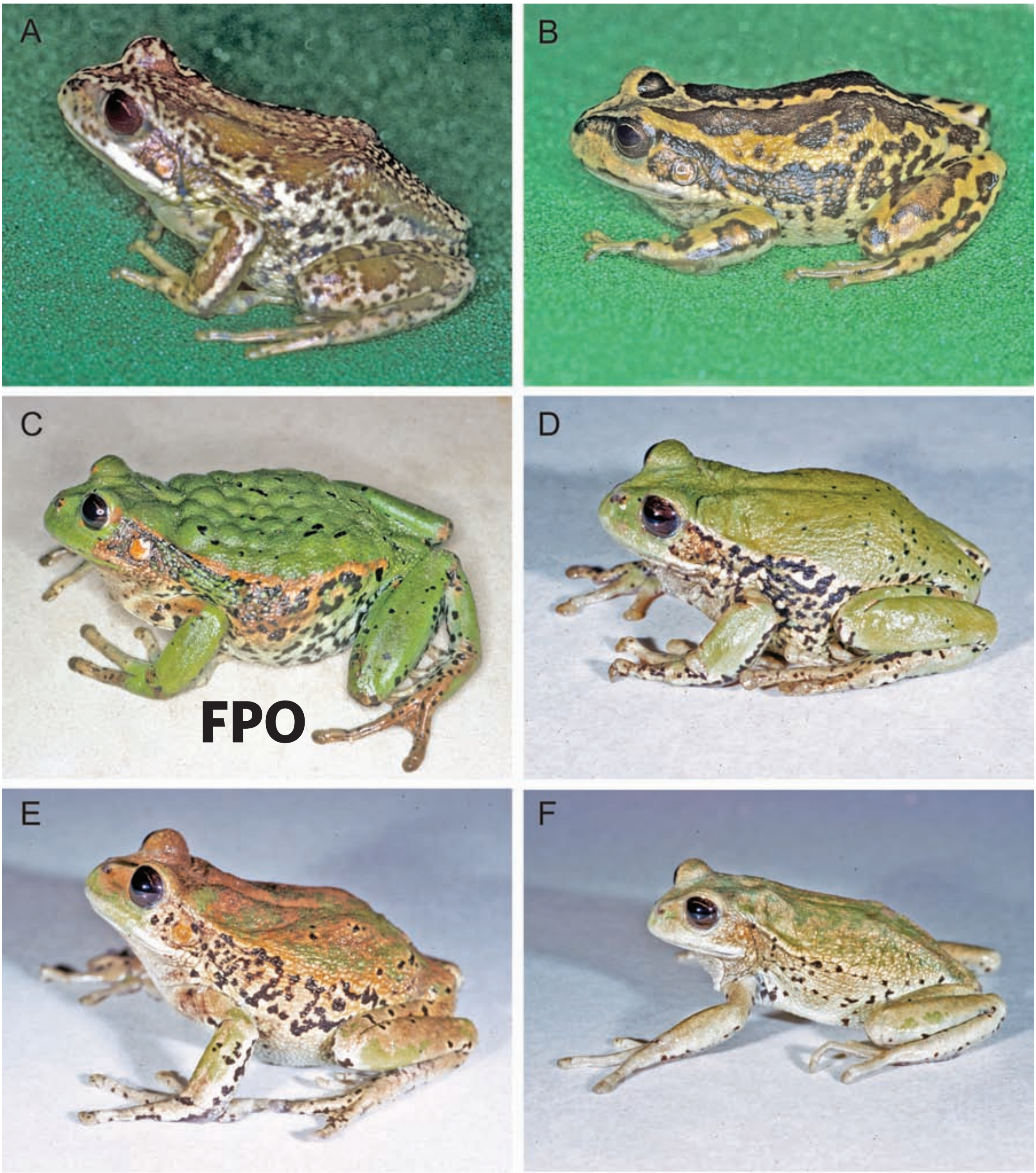

Fig. 11.24 *Gastrotheca riobambae*. A: KU 120758, male, 40.1 mm SVL, 15 km E Riobamba, Chimborazo, Ecuador. B: KU 120725, male, 42.4 mm SVL, same locality. C: KU 139139, female, 59.5 mm SVL. D: KU 148530, male, 51.1 mm SVL. E: KU 148533, female, 62.2 mm SVL. F: KU 148531, male, 54.9 mm SVL. C–F from Lago Cuicocha, 3070 m, Imbabura, Ecuador. Photos by J. D. Lynch (A) and W. E. Duellman (B–F), KUDA.

rahua.—The dorsum is brown, with reddish-brown markings edged with black. The flanks are green. The posterior surfaces of the thighs are gray or green, with faint yellowish-cream spots (J. D. Lynch field notes, 23 June 1968).

KU 138577–86 from Quiroga, Provincia de Imbabura.—The dorsum in half of the specimens is uniformly bright green; in others it is pale brown, with or without chocolate-brown or green blotches. All have a dark bronze stripe from the eye to the midlateral portion of the body, and an equal suffusion on the flanks and posterior surfaces of the thighs, with black spots on latter. The venter is beige white, with grayish-black markings (T. H. Fritts field notes, 24 July 1970).

KU 138537–613 from Otavalo, Provincia de Imbabura.—The dorsum in some is uniformly yellowish green; in others it is tan, pale brown, or bronze, with or without bronze-brown or yellowish-green blotches. The flanks are bronze, with a green suffusion anteriorly and a bluish-gray suffusion posteriorly. The posterior surfaces of the thighs are beige, with a pale green suffusion and, in some specimens, black spots (T. H. Fritts field notes, 25 July 1970).

KU 139136–39 from Lago Cuicocha, Provincia de Imbabura.—The dorsum is green. The flanks are predominately green, mottled with black and cream or bronze. The groin is pale blue. The posterior surfaces of the thighs are blue, with black reticulations. The venter is dull grayish white, with black markings. In one juvenile the dorsum is bronze tan. The flanks and hidden surfaces of the thighs are pale greenish yellow, with black spots; the venter is pale yellow, with black reticulations (W. E. Duellman field notes, 30 January 1971).

KU 142627–30 from Baños, Provincia de Tungurahua.—The dorsum is tan or green, with darker brown or green markings. The groin is gray, with black mottling. The posterior surfaces of the thighs are gray, tan, or green, with black mottling; the venter is dirty gray, with black spots (W. E. Duellman field notes, 27 July 1971).

KU 164235–37 from Lago Yahuarcocha, Provincia de Imbabura.—The dorsum is brown, with darker brown markings edged with tan. The flanks are cream, with brown mottling. The posterior surfaces of the thighs are dark brown, with cream mottling. The venter is cream, with pale brown flecks and mottling; the throat is gray. In one juvenile the dorsum is uniformly bright green (W. E. Duellman field notes, 4 October 1974).

Nearly all specimens of *Gastrotheca riobambae* have well-defined dark (gray or black) spots or reticulations on the venter of the body and hind limbs. Descriptions of the color of the iris in life vary from reddish brown to reddish bronze to copper, all with black reticulations.

Data are available on the colors of two lots of young and their mothers (KU 204033–34, from 7 km N Latacunga, Provincia de Cotopaxi). Both females were pale green, with brown markings. Of 30 young that metamorphosed from one lot of tadpoles, 21 were green with dark green markings, and 9 were tan with dark green markings. In a second lot of 39 young, 26 were green with dark green markings, and 13 were brown with green markings.

Hoogmoed (1967) observed ontogenetic changes in coloration in captive-raised juveniles. Some individuals that had green markings on a green dorsum changed to a uniform green, whereas in others the green blotches changed to brown. These observations, together with the variation in dorsal coloration in each population of *G. riobambae*, indicate that dorsal coloration is a poor descriptor for the species.

MEASUREMENTS

The means of all measurements of females are significantly larger than those of males (Table 11.12).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous fine vermiform pattern. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasals articulate at the anterolateral margin of the frontoparietals. The frontoparietals have a complete articulation medially; each bears a narrow supraorbital flange and a moderate-sized otic flange. A temporal arcade is absent. The frontoparietal covers the anterior epiotic eminence and part of the posterior epiotic eminence, and is partially fused to them; thus the carotid canal is partially open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for more than three-fourths the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a broad overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The postorbital process of the maxilla is massive, and has a broad horizontal articulation with the wide zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the narrow otic plate articulates marginally with the crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in length, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has an acuminate terminus anterior to the level of the neopalatines. The sphenethmoid is ossified posterior to the midlength of the orbit, but is not synostosed with the prootic. The neopalatines are

Table 11.12 Univariate statistics for adults of *Gastrotheca riobambae*. Differences between the means of the sexes for all measurements are significant (ANOVA, $P \leq 0.01$).

	Males ($n = 81$)			Females ($n = 106$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	43.0	34.1–56.8	4.87	48.6	33.3–66.4	7.58
Tibia length	17.5	14.2–24.1	2.02	20.0	13.9–27.8	3.14
Foot length	18.5	14.6–26.3	2.45	21.8	14.7–31.9	3.81
Head length	14.0	11.2–17.8	1.40	15.9	11.1–23.2	2.17
Head width	15.7	12.7–19.9	1.47	17.6	12.1–31.5	2.72
Interorbital distance	3.9	3.2–5.3	0.46	4.4	3.1–6.9	0.79
Eyelid width	3.3	2.6–4.2	0.37	3.6	2.6–5.2	0.47
Internarial distance	2.4	1.7–3.6	0.39	2.8	1.5–4.0	0.50
Eye diameter	4.0	3.1–5.4	0.46	4.4	3.5–6.1	0.63
Eye–nostril distance	3.3	2.5–4.5	0.42	3.7	2.7–4.9	0.47
Orbit–jaw distance	2.3	1.7–3.2	0.35	2.6	1.5–3.6	0.47
Nostril–jaw distance	2.9	2.3–4.0	0.37	3.3	2.1–4.8	0.58
Tympanum diameter	2.2	1.7–3.0	0.27	2.5	1.6–3.5	0.42
Thumb length	7.9	5.9–12.1	1.13	9.3	5.9–19.6	1.92
Third finger length	13.3	9.9–19.8	1.86	15.4	10.3–23.4	2.90
Disc width	1.8	1.0–3.1	0.37	2.0	1.3–3.3	0.44

moderately separated medially, and are smooth ventrally. The pterygoid articulates with the medial surfaces of the zygomatic ramus of the squamosal and the postorbital process of the maxilla via a long acuminate recurved process on the anterior ramus of the pterygoid. The vomers bear small dentigerous processes located between the middle quadrants of the choanae.

Life History

Gastrotheca riobambae produces eggs that hatch as tadpoles, which complete their development in shallow ponds. Twelve brooding females having snout–vent lengths of 44.3–62.2 mm ($\bar{x} = 50.3$) contained 64–166 eggs ($\bar{x} = 121$), of which the diameter of the ova or embryos was 2.7–5.6 mm ($\bar{x} = 4.0$). The number of eggs corresponds with the mean number of 128 in 21 clutches reported by del Pino and Escobar (1981). Brooding females have been found in January–September, which corresponds to the rainiest time of the year in the Andes of Ecuador. Eugenia del Pino (pers. comm.) has observed several females for seven years in an outdoor enclosure in Quito; each female breeds only once each year.

Observations on the mating behavior in captive individuals by Harrison Matthews (1957), Deckert (1963), and Hoogmoed (1967) indicate that mating takes place on land. Subsequent to the initiation of amplexus, the female twists her hind limbs and in so doing elevates the cloacal region to a level equal to or above the opening of the pouch. The male produces fluid, which presumably contains sperm, from the cloaca; he uses his feet to wipe this fluid over the female from her cloaca to the opening of the pouch. As eggs are extruded by the female, the male directs the eggs into the pouch with his feet.

Recently fertilized eggs are uniformly pale yellow; the mean ovum diameter is 1.9 mm (del Pino and Escobar, 1981). Shortly after placement of the eggs in the pouch, the female seeks a secluded place, usually under a stone. The female presses her back against the stone; this behavior results in the distention of the pouch and the arrangement of the eggs in one or two uniform layers in the pouch (del Pino, 1983).

Del Pino and Escobar (1981) presented a detailed developmental table for embryos of *Gastrotheca riobambae*. Incubation time in 16 females was 70–108 days ($\bar{x} = 87 \pm 9$). Near the end of incubation the aperture of the pouch opens and, when the tadpoles hatch, the female moves to water. The parturition of tadpoles is partly spontaneous and partly assisted by the female, who distends the pouch opening with her hind feet and inserts one or both hind feet into the pouch to pull out the tadpoles (Fig. 7.16).

Newly released tadpoles are in Stage 33, with small limb buds; they are active swimmers and begin feeding after one or two days. According to del Pino and Escobar (1981), the vitelline envelope and jelly capsule rupture during birth and the tadpole straightens. Oral suckers are absent. Circulation through the external gills terminates almost immediately after the tadpole enters water, but the gills are not retracted into the opercular chamber until about a day after hatching. Within the opercular chambers, the gills reduce in size and finally disappear in about one week.

The duration of larval development is highly variable and probably is dependent on temperature and the availability of food. Del Pino and Escobar (1981) noted that in Quito, where tadpoles were maintained at an average temperature of 17°C, 4–12 months were required for larval development. Hoogmoed (1967) maintained tadpoles at 20°C–26°C, and metamorphosis occurred 41 days after hatching; Walker (1957) reported 66 days. Tadpoles from Latacunga maintained in my laboratory at 20°C–22°C and fed ad libitum (with food available at all times) on boiled lettuce and fish food metamorphosed in 51–60 days after hatching. The ranges of snout–vent lengths of metamorphosing young are 22.1–24.5 mm ($\bar{x} = 23.1$, $n = 6$) from Quito and 22.7–25.4 mm ($\bar{x} = 23.9$, $n = 13$) from Latacunga. Hoogmoed (1967) noted that males raised in captivity began calling 85 days after metamorphosis, and that a female developed ovarian eggs 145 months after metamorphosis. The diverse data suggest that males may breed during the first season after metamorphosis, but that females require an extra year to reach sexual maturity.

Numerous papers have been published on the developmental biology of *Gastrotheca marsupiata*. Works by Harrison Matthews (1957), Walker (1957), Grenard (1958), Oeser (1959), Brenner (1960), Weiss (1960), Deckert (1963), Kästle (1963), Hoogmoed (1967), and Spannhof and Spannhof (1971) all cite Quito as the source of their specimens. If the specimens actually came from Quito, the studies are based on *G. riobambae*. *G. pseustes*, which closely resembles *G. riobambae*, occurs in the Andes surrounding Quito, so possibly some of the above works are based on *G. pseustes*. I have examined the specimens (RMNH 1895, 14967, 14990) on which Hoogmoed (1967) based his observations and have confirmed their identity as *G. riobambae*. Del Pino and Escobar (1981) stated that most of their specimens came from the vicinity of Machachi, but that frogs from other localities in the provinces of Cotopaxi, Pichincha, and Tungurahua also were used. Both *G. riobambae* and *G. pseustes* occur at Machachi, and *G. pseustes* is found in the Andes in the provinces mentioned, so it is most probable that the developmental work by del Pino and her associates has been based on both species. The tadpole described and figured as *G. riobambae* by Wassersug and Duellman (1984) is *G. pseustes*.

Tadpoles

Some tadpoles grow to a large size—30 mm in body length and 90 mm in total length—but the maximum for most individuals is 25 mm in body length and 75 mm in total length. A typical tadpole in Stage 28 (KU 148591) has a body length of 18.5 mm and a total length of 43.0 mm. In dorsal view the body is ovoid, with a slight constriction just posterior to the orbits, and is widest posteriorly; the snout is rounded. In profile the body is highest posteriorly; the height is equal to about two-thirds the width of the body; the snout is bluntly rounded. The throat is slightly concave. The eyes are large, and are directed dorsolaterally. The interorbital distance is about one-third the width of the body at the level of the orbits. The nostrils are midway between the eyes and the tip of the snout, and are directed anterolaterally. The spiracular tube is short and sinistral, with the opening directed posterodorsally on the ventrolateral surface at a point slightly posterior to midlength of the body. The cloacal tube is short, conical, and median, with a transverse opening. The caudal musculature is moderately slender; it is shallower than the dorsal fin at midlength of the tail. The musculature terminates gradually in a pointed tip well within the margin of the caudal fin. The dorsal fin arises gradually from the posterior edge of body. The dorsal and ventral fins are equal in depth, and terminate in a rounded tip.

The width of the oral disc is about 40% of the width of the body. The disc is bordered laterally and ventrally by two alternating rows of small marginal papillae. There are two upper and three lower rows of labial teeth; the tooth rows are about equal in length; the first lower row is narrowly interrupted medially. The upper jaw sheath is slender, in the form of a continuous arch; the lower sheath is moderately robust, and is broadly V-shaped. Both sheaths have small pointed serrations.

The caudal musculature and dorsum of the body are grayish brown, with fine brown flecks. The belly is gray; the fins have brown reticulations.

Advertisement Call

The call consists of a low-pitched pulsed note (± 1480 Hz); this primary note is followed by two or more shorter notes that form the territorial call (Fig. 6.8B).

Distribution and Ecology

This species is widely distributed in the inter-Andean basins in central and northern Ecuador, from Ibarra and Otavalo in the north to the Riobamba Basin in the south (Fig. 11.25). In these basins it occurs at elevations of 2500–2900 m. From the Ambato Basin it descends

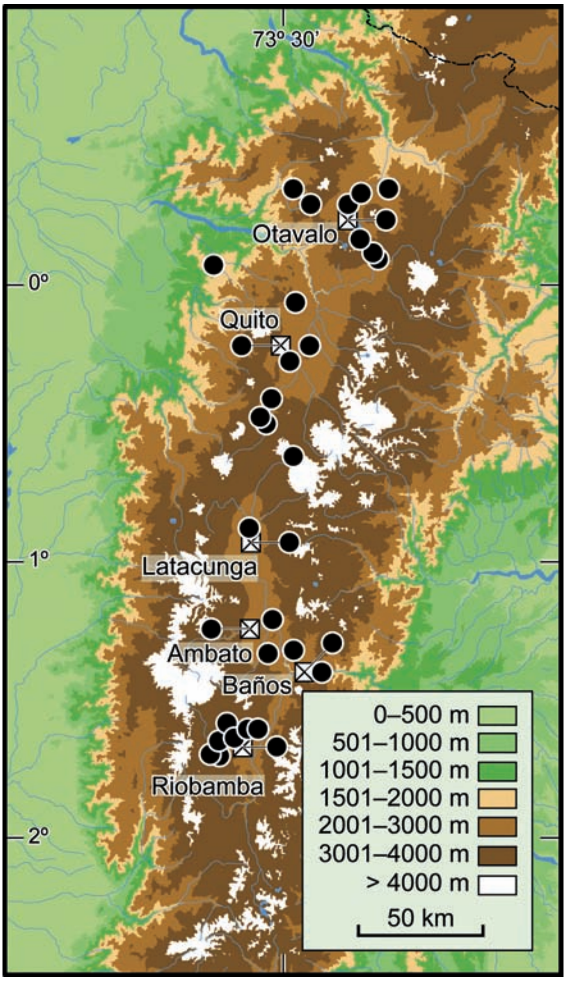

Fig. 11.25 Andean region of Ecuador and southern Colombia, showing the localities of known occurrences of *Gastrotheca riobambae*.

the valley of the Río Pastaza to a point below Baños at an elevation of 1590 m. South of Riobamba it occurs in a valley at an elevation of 3220 m, and at Machachi it is found at 3120 m; in the northern part of its range it occurs at Laguna Cuicocha at an elevation of 3070 m.

Throughout most of its range, *Gastrotheca riobambae* inhabits cultivated areas; there it occurs in drainage ditches and takes refuge in stone walls and rock piles during the day. The species is not uncommon in gardens and parks in cities, and individuals can be heard calling at night in towns ranging in size and elevation from Baños (1800 m) to Quito (2840 m). At Laguna Cuicocha, by day *G. riobambae* were located in large terrestrial bromeliads, and in various parts of the range individuals have been found in large *Agave* by day. Tadpoles have been observed in drainage ditches, cisterns, and shallow grassy ponds.

This species essentially is parapatric to *Gastrotheca espeletia*, which is found in the páramos to the north of Río Chonta, and to *G. pseustes*, which occurs in the cordilleras to the east and west of the inter-Andean basins inhabited by *G. riobambae*. At Machachi (elevation 3120 m) at the southern edge of the Quito Basin, *G. riobambae* apparently occurs in sympatry with *G. pseustes*. Of 29 specimens (USNM 205807–35) collected there by Roy W. McDiarmid, three clearly are *G. riobambae* and 26 are *G. pseustes*.

Conservation Status

In the IUCN Red List, *Gastrotheca riobambae* is categorized as Endangered. Although this was a common species in the 1970s, populations have declined throughout its range. Probably some of the decline relates to habitat loss, but agrochemical pollution of the water in irrigation ditches, which are most frequently inhabited by tadpoles, probably is the major cause for declines.

Etymology

The specific name *riobambae* refers to the type locality, which is Riobamba, Ecuador.

Remarks

The variation in this species was analyzed by comparing morphometric and descriptive characters in samples from five inter-Andean basins (designated, from north to south, as Otavalo, Quito, Latacunga, Ambato, and Riobamba), from Baños on the eastern slopes of the Andes, and from Lago Cuicocha in the Cordillera Occidental (Table 11.13 and Fig. 11.26).

Table 11.13 Numbers of specimens of *Gastrotheca riobambae* from different populations used in the analyses. The morphometric analyses were based only on adults; the analyses of descriptive characters and color pattern were based on all specimens.

Population	Males	Females	Subadults	Total
Cuicocha	7	16	2	25
Otavalo	21	7	5	33
Quito	5	11	0	16
Latacunga	5	6	1	12
Ambato	2	9	2	13
Baños	11	27	0	38
Riobamba	30	30	12	72
Totals	81	106	22	209

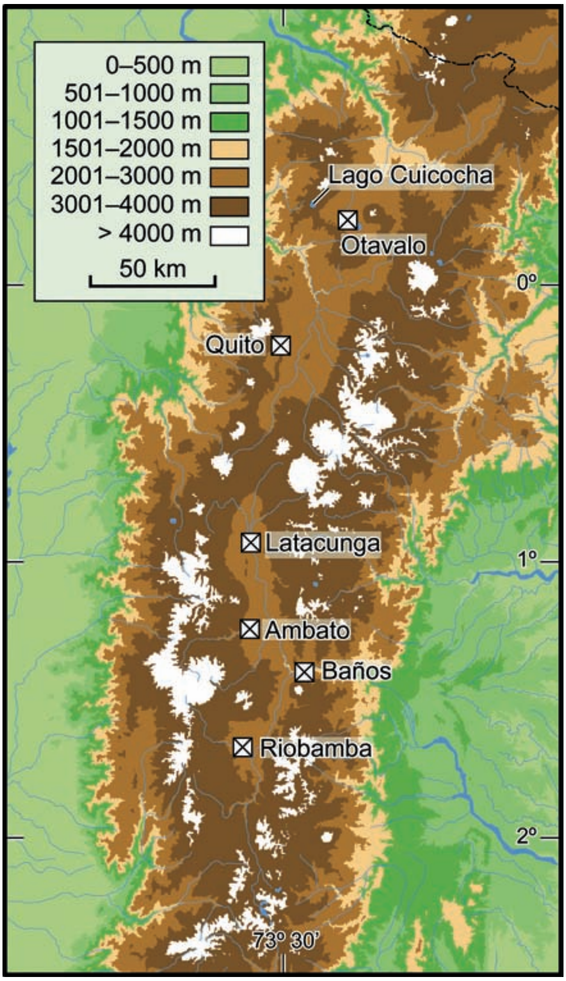

Fig. 11.26 Andean region of Ecuador, showing the localities from which samples were used in the discriminant functions analysis of morphometrics.

MORPHOMETRICS

An analysis of variance showed that sexual dimorphism was evident in all measurements except eyelid width in those samples containing large numbers of specimens (Cuicocha, Riobamba, Baños); this was verified by non-parametric tests. The analysis of variance also showed sexual dimorphism in foot length in the sample from Quito, and in head length in the sample from Latacunga. The apparent absence of sexual dimorphism in these samples presumably is an artifact of the small sample size. When all of the samples were pooled, significant differences between the sexes were evident in the means of all measurements (Table 11.14). Moreover, a principle components analysis showed that sexual dimorphism is strictly size related, with no significant shape component; all variables fell out on the first canonical axis, with extremes being in snout–vent length, foot length, and head width.

Table 11.14 Snout-vent lengths in seven samples of *Gastrotheca riobambae*. The first line = *n*; the second line = range, and the third line = mean ± 1 standard deviation.

Population	Males	Females
Cuicocha	7	16
	51.0–56.8	47.6–66.4
	53.7 ± 2.37	40.1 ± 4.33
Otavalo	21	7
	34.1–48.0	33.3–46.3
	39.6 ± 3.61	40.1 ± 4.33
Quito	5	11
	43.3–50.1	38.8–55.0
	46.3 ± 3.83	44.5 ± 3.12
Latacunga	5	6
	38.7–49.5	39.1–52.1
	43.3 ± 3.83	44.5 ± 3.12
Ambato	2	9
	43.6–46.5	34.4–59.0
	45.1 ± 2.05	49.2 ± 7.20
Baños	11	27
	43.0–50.4	40.4–65.0
	45.9 ± 2.10	47.7 ± 4.90
Riobamba	30	30
	30.9–46.3	33.7–57.9
	39.8 ± 3.84	43.7 ± 6.15

Geographic variation in snout–vent length is evident among the seven populations. The largest frogs are from the northernmost population at Cuicocha, whereas the smallest are from the geographically proximal population at Otavalo and from the southernmost population at Riobamba (Table 11.14). The geographically intermediate populations (Quito, Latacunga, Ambato, plus Baños) are rather uniform in snout–vent length. A stepwise discriminant functions analysis (jackknifed eight-step model) revealed that there is considerable overlap in all populations, except that the sample from Cuicocha has only minimal overlap with two populations: Quito and Riobamba (Fig. 11.27).

STRUCTURAL CHARACTERS

The texture of the dorsal skin was characterized as smooth in 95 specimens from all samples except Cuicocha, areolate in 104 specimens from all samples (including all specimens from Cuicocha), and granular in 10 specimens from Latacunga and Riobamba. The webbing on the foot extends to the distal tubercle on the fourth toe in 114 specimens, and to a point midway between the penultimate and distal tubercles in 87 specimens; these conditions are present in all samples.

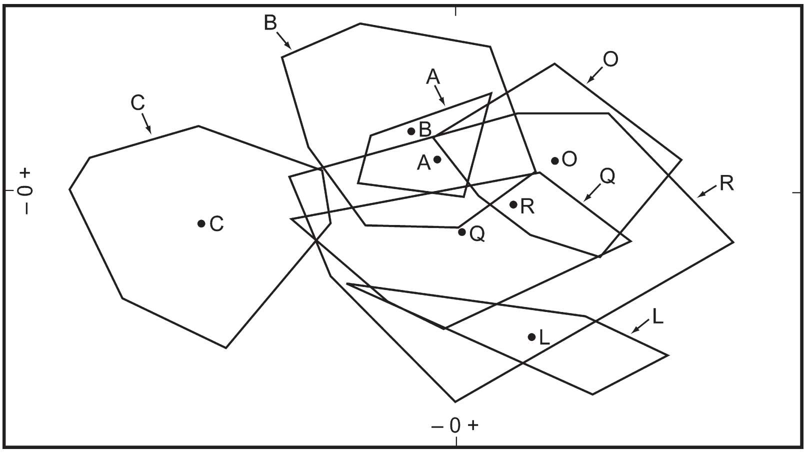

Fig. 11.27 Multivariate plot of a stepwise discriminant analysis of morphometrics of *Gastrotheca riobambae* from seven localities in the Ecuadorian Andes (see Fig. 11.26). Polygons encompass the dispersion of individuals; dots are the means of samples identified by the letters A = Ambato (*n* = 13), B = Baños (*n* = 38), C = Cuicocha (*n* = 25), L = Latacunga (*n* = 12), O = Otavalo (*n* = 12), Q = Quito (*n* = 16), and R = Riobamba (*n* = 72).

Eight specimens from Otavalo and Riobamba have the webbing extending only to the penultimate tubercle on the fourth toe. The fifth toe is webbed to the distal tubercle in 198 specimens, and to a point midway between the penultimate and distal tubercles in 11 specimens.

A pale labial stripe is present and a dark canthal stripe is absent in all specimens from Cuicocha; the opposite conditions exist in specimens from other populations. The dorsum is either grayish tan to pale brown or pale to dark green, usually with darker brown or green markings (absent in 12 specimens from all populations except Ambato and Latacunga). The dorsal markings consist of dark longitudinal paravertebral marks in 169 specimens; some individuals from all populations lack these marks, and the marks are absent from all specimens from Ambato and Baños. A narrow dark middorsal stripe is present in 1 specimen from Cuicocha, and a broad middorsal stripe is present in 4 specimens from Riobamba. A dark interorbital bar is present in 2 specimens (Quito and Riobamba). In addition to the large dark markings, black flecks are present on the dorsum in 10 specimens from Cuicocha and 4 from Riobamba. A pale dorsolateral stripe is present in 56 specimens from all populations (including all individuals from Otavalo) except Ambato and Latacunga.

The flanks have dark mottling or spots in all specimens (except 1 from Riobamba); the groin and anterior surface of the thigh are pale blue with black spots in all specimens from Cuicocha, whereas the groin is white with black spots or mottling in other specimens. The posterior surface of the thigh is uniformly bluish gray or brownish gray in 78 specimens from all populations, and marked with dark spots in the others. A pale supracloacal stripe is present in 130 specimens; it is lacking in some individuals from all populations and from all specimens from Cuicocha. In breeding males the throat is gray. Otherwise the chest and belly are uniformly pale in 7 specimens (1 each from Baños, Latacunga, and Riobamba, and 4 from Otavalo); all others have dark markings. Generally the markings are in the form of bold mottling in specimens from Otavalo and Riobamba, faint mottling in those from Cuicocha, and spots in those from other populations. The pattern on the ventral surface of the shank is the same as that on the belly.

The frogs from Cuicocha are the most divergent morphometrically and in coloration among the seven populations. The variation exhibited by the frogs in the other six populations presents a mosaic that shows no consistent geographic trends. The recognition of these frogs as representatives of a single species is corroborated by the absence of allozymic differentiation among the populations (Duellman and Hillis, 1987); furthermore, in an analysis of four genes from samples throughout the range, the sample from Lago Cuicocha was not distinguished genetically from samples from other populations.

The populations referred to *Gastrotheca riobambae* include the type localities of four nominal taxa of *Gastrotheca*. Fowler (1913) named *Hyla riobambae* from Riobamba and *H. quitoe* from Quito. The holotype of *H. riobambae* (ANSP 16161) is a male having a snout–vent length of 48.3 mm; the color pattern and morphological characters are encompassed by the variation displayed by his sample from the Riobamba Basin. The holotype of *H. quitoe* (ANSP 18235) is a juvenile having a snout–vent length of 18.8 mm. This specimen is desiccated, and no color pattern is evident; Fowler's illustration (1913, pl. 7) shows a color pattern common among juveniles from Quito. Acting as first revisers, Duellman and Fritts (1972) selected *H. riobambae* as having priority over *H. quitoe*, because (1) *H. riobambae* has page priority, (2) the holotype of *H. riobambae* is an adult in good condition, and (3) the holotype of *H. quitoe* is a juvenile in poor condition.

Chorophilus olivaceus was named by Andersson (1945) from "Rio Napo, 400 m," Ecuador. As noted by Duellman and Fritts (1972), the holotype (NHRM 1965) is a male *Gastrotheca* having a snout–vent length of 41.7 mm. This specimen probably came from Baños, an area frequented by the collector, William Clarke-MacIntyre. The size, proportions, structural characters, and coloration all are encompassed by the variation in the sample from Baños.

Gastrotheca cavia was named by Duellman (1974) from islands in Lago Cuicocha. The species was distinguished from *G. riobambae* by its larger size and color pattern. Individuals having the same coloration as those on the islands have been found on the shores of Lago Cuicocha, but these are smaller than individuals from the islands. Because no allozymic differences were found between samples from the islands, the shore of the lake, and other populations referred to *G. riobambae*, Duellman and Hillis (1987) considered *G. cavia* to be a junior synonym of *G. riobambae*. Subsequent analyses of mitochondrial and nuclear genes support their conclusion.

Gastrotheca (*Duellmania*) *ruizi* Duellman and Burrowes

Gastrotheca ruizi Duellman and Burrowes, 1986:2.—Holotype: KU 200000 from Santiago, 2250 m, Município de Mocoa, Departamento de Putumayo, Colombia.

Diagnosis

This large species attains a maximum snout–vent length of 78.0 mm. The tibia length is less than 50% of the snout–vent length, and is slightly shorter than the foot. The interorbital distance is slightly greater than the width of the upper eyelid. The skin on the dorsum is smooth, not co-ossified with skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is longer than the second. The discs are slightly wider than the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is dull green or brown, with darker spots. There are no markings on the head. The flanks are uniformly brown or gray; the venter is dark gray.

Gastrotheca ruizi is distinctive in having an acuminate protruding snout, and a dark dorsum with pale green longitudinal paravertebral marks. It is like *G. orophylax* in having a bronze tympanum, but otherwise *G. orophylax* is uniformly green and has a truncate snout. Superficially, *G. ruizi* resembles *G. psychrophila*, but the latter differs by having a rounded snout and by lacking paravertebral green marks.

Description

The following description is based on 19 specimens. The body is robust. The maximum snout–vent length is 67.4 mm in males, and 78.0 mm in females. The head width is slightly less than the head length. In dorsal view the snout is acuminate; in profile it is continuously inclined from the nostrils to the tip. The canthus rostralis is angular in cross-section. The loreal region is slightly concave; the lips are thin and rounded. The top of the head is concave between the elevated lateral edges of the frontoparietals. The interorbital distance is about 110% of the width of the upper eyelid. The internarial area is slightly concave. The nostrils are barely protuberant, and are directed dorsolaterally at a point below the anterior terminus of the canthus rostralis and well behind the anterior margin of the lower jaw. The diameter of the eye is slightly greater than its distance from the nostril. The tympanum is vertically ovoid, and is separated from the eye by a distance twice the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately heavy, and extends from the posterior corner of the orbit to a point above the axilla.

The arm is robust, and lacks ulnar tubercles. The hand is moderate in size. The fingers are long and unwebbed. The discs on the fingers are small and round; the width of the disc on the third finger is slightly less than the length of the tympanum. The first finger is longer than the second. The relative lengths of the fingers are II < I < IV < III. The subarticular tubercles are small, round, and moderately low; the few supernumerary tubercles are small, and are present only on the proximal segments of the fingers. The palmar tubercle is bifid; the prepollical tubercle is large, elongate, and ovoid; in breeding males the thumb bears a brown nuptial excrescence. The hind limb is moderately short and robust. The tibia length is about 44% of the snout–vent length; the foot length is slightly greater than the tibia length. A calcar, outer metatarsal tubercle, and tarsal folds are absent. The inner metatarsal tubercle is moderately large, ovoid, and visible from above. The toes are long. The relative lengths of the toes are I < II < III < V < IV. The toes are about two-fifths webbed; the webbing formula is **I**2^{-}—2^{+}**II**2^{-}—3**III**2—3^{+}**IV**3—2**V**. The subarticular tubercles are small and round; the supernumerary tubercles are small, subconical, and present only on the proximal segments.

The skin on the dorsum of the head, body, and limbs is smooth; the skin on the flanks is areolate; the skin on the belly and ventral surfaces of the thighs is granular. Eyelid tubercles are absent. Cloacal folds and tubercles are absent. The opening of the brood pouch is U-shaped, with the anterior border at the level of the sacrum. The dentigerous processes of the vomers are small, transversely ovoid, and widely separated medially at the level of the posterior margins of the small quadrangular choanae. Each process bears four or five teeth.

COLOR IN PRESERVATIVE

In most specimens the dorsum is dark bluish gray, with a narrow middorsal and broad dorsolateral pale bluish-gray stripes. The flanks, anterior and posterior surfaces of the thighs, and feet are dark gray to dark brown. One female (KU 200303) has a dull tan dorsum and flanks. The upper flanks are finely mottled with black.

COLOR IN LIFE

The general appearance of living *Gastrotheca ruizi* is of a green frog that may be darker green or brown middorsally, and have dark brown flanks (Fig. 11.28). The following are detailed color notes of living topotypes (KU specimens from Santiago, Departamento de Putumayo, Colombia).

KU 200000.—The dorsum is dark green medially and pale green laterally. The top of the head and loreal region are pale green. The tympanum is bronze. The dorsal surfaces of the thighs are greenish brown; the posterior surfaces of the thighs are grayish brown, with a tint of dark blue. The throat is yellow; the belly is dull cream; the ventral surfaces of the limbs are creamy gray. The iris is a dull greenish bronze, with fine black reticulations.

KU 200001 and 200003–5.—These have the same coloration as above, but have a narrow bronze line separating the dorsal color from that of the flanks; the groin and anterior and posterior surfaces of the thighs are pale blue.

KU 200002.—The dorsum is dark brown, with bronze middorsal and dorsolateral lines; the lateral part of the dorsum is pale green.

KU 200303.—The dorsum is greenish tan, with diffuse brown dorsolateral areas. An irregular bronze dorsolateral line extends to the groin. The flanks are mottled bronze tan and brown; the limbs are brown. The venter is grayish cream, with a blue suffusion in the axilla and groin (P. A. Burrowes field notes, 25 February 1984).

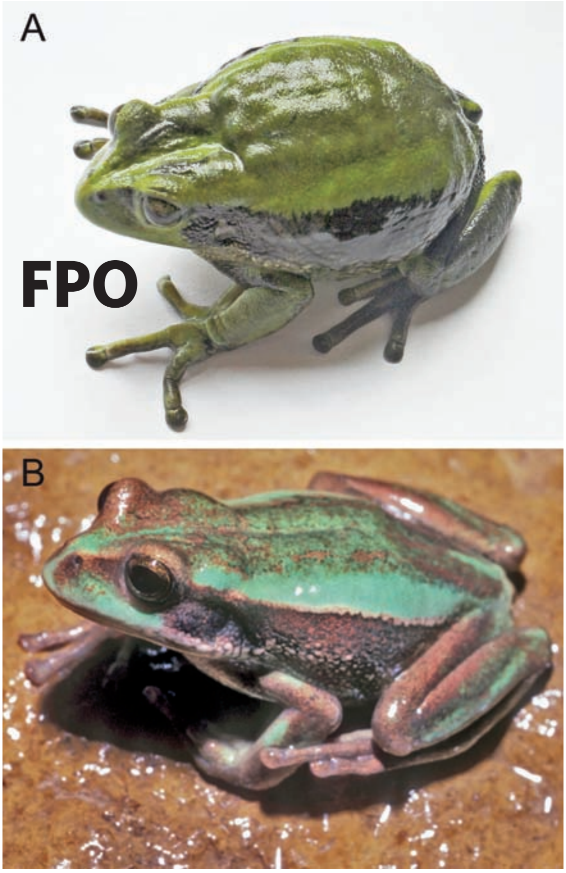

Fig. 11.28 *Gastrotheca ruizi*. A: female, 83.5 mm SVL, San Miguel, Putumayo, Colombia. B: KU 200004, male, 60.3 mm SVL, Santiago, Putumayo, Colombia. Photos by J. E. Pérez V. (A) and W. E. Duellman (B), KUDA.

A photograph of a juvenile shows a cream-colored flank, with irregular dark brown markings (Estupiñán, 2004).

MEASUREMENTS

Females are noticeably larger than males (Table 11.15).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous coarse pit-and-ridge pattern. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasals articulate at the anterolateral margin of the frontoparietals. The frontoparietals have a complete articulation medially; each

Table 11.15 Univariate statistics for adults of *Gastrotheca ruizi*

	Males ($n = 11$)			Females ($n = 4$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length**	59.4	53.5–67.4	4.42	69.8	62.1–78.0	7.24
Tibia length**	26.8	24.9–30.0	1.47	30.7	28.8–33.2	1.86
Foot length**	28.2	25.8–32.7	1.83	32.0	30.9–33.5	1.11
Head length	20.0	18.4–21.6	1.14	24.1	20.9–29.9	4.23
Head width	20.4	18.8–21.8	1.03	22.8	20.4–26.1	2.40
Interorbital distance	5.1	4.4–5.8	0.48	5.6	4.6–6.3	0.77
Eyelid width	4.0	3.0–5.1	0.54	4.4	4.0–4.8	0.39
Internarial distance	3.8	3.0–4.7	0.59	4.0	3.8–4.4	0.29
Eye diameter	5.3	4.4–7.0	0.78	5.6	5.0–6.1	0.46
Eye–nostril distance	4.6	4.1–5.4	0.41	5.3	4.8–5.5	0.34
Orbit–jaw distance	3.6	3.2–4.0	0.29	4.0	3.5–4.8	0.57
Nostril–jaw distance	4.3	3.9–5.0	0.35	4.7	4.5–5.0	0.22
Thumb length**	11.2	9.6–12.5	0.99	13.3	11.5–14.3	1.22
Third finger length	19.5	17.7–22.2	1.22	21.4	20.2–23.0	1.17
Disc width	2.6	2.0–3.5	0.54	3.1	2.3–3.8	0.62

**Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

bears a wide supraorbital flange and a small otic flange. A temporal arcade is absent. The frontoparietal does not cover the epiotic eminences; thus the carotid canal is partially open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at an angle greater than 46°. The premaxillae bear long spinous medial processes. The preorbital process of the maxilla is visible; the pars facialis of the maxilla articulates with the dorsally adjacent nasal for about the length of the rostrum. The pars facialis is not distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The postorbital process of the maxilla is massive, and has a broad diagonal articulation with the wide zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the narrow otic plate articulates marginally with the crista parotica. The dorsal part of the stapedial footplate is two to three times the length of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has an acuminate terminus anterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are moderately separated medially, and bear a ventral flange. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a long acuminate recurved process on the anterior ramus of the pterygoid. The vomers bear small dentigerous processes located between the posterior quadrants of the choanae.

Life History

Breeding is known to occur in February. Two brooding females were found in February 1984; one of these produced 134 tadpoles on 7 March. One of the tadpoles metamorphosed in 108 days, with a snout–vent length of 28.0 mm. This individual (KU 200015) was colored much like the adults, except that the green color was more intense. The shanks and feet were bronze brown, with a green longitudinal stripe on the foot. The lower flanks were cream, with a bronze-brown tint; the upper flanks were dark brown. The venter was creamy white; the labial stripe was white. The iris was coppery bronze. A brooding female found in January 2012, having a snout–vent length of 83.5 mm, gave birth to 119 tadpoles on 19 March (P. Villota, pers. comm.).

Tadpoles

A tadpole in Stage 38 (KU 200014) has a body length of 24 mm, and a total length of 66.5 mm. In dorsal view the body is ovoid, and is widest at midlength; the snout is round. In profile the body is highest at about two-thirds the length of the body; its height is about equal to two-thirds the width of the body; the snout is inclined from the nostrils to the tip. The throat is convex. The eyes are large, and are directed dorsolaterally. The interorbital distance is less than one-third the width of the head at the level of the orbits. The nostrils are slightly closer to the eyes than to the tip of the snout, and are directed anterolaterally. The opening of the spiracular tube is at midlength of the body. The cloacal tube is sinistral, long, conical, and has a transverse opening. The caudal musculature is moderately high; its height is equal to that of the dorsal fin at midlength of the tail. The musculature tapers to a point just short of the tip of the caudal fins. The dorsal fin arises gradually from the posterior edge of the body, is slightly shallower than the ventral fin, and terminates in a rounded tip.

The width of the oral disc is equal to about half the greatest width of the body. The disc is bordered by a single row of short blunt marginal papillae. There are two upper and three lower rows of labial teeth; the tooth rows are about equal in length; the first lower row is narrowly interrupted medially. The upper jaw sheath forms a continuous arch; the lower sheath is moderately massive, and is broadly V-shaped. Both sheaths bear fine pointed serrations.

The caudal musculature and dorsum of the body are pale brown. The belly is grayish tan. Dark brown markings on the tail consist of a longitudinal row of large flecks on the dorsal and ventral fins, a dorsolateral stripe on the caudal musculature, and a midlateral line on the proximal one-third of the musculature.

Advertisement Call

The mating call consists of a primary note, “wraaack,” usually followed by two or three secondary notes, “ack-ack-ack.”

Distribution and Ecology

This species is known from several localities, at elevations of 2040 and 2319 m in the Valle de Sibundoy on the eastern slopes of the Cordillera Oriental in southern Colombia (Fig. 11.5). On 25 February 1984, *Gastrotheca ruizi* were 1–2 m above the water, calling from branches of small bushes in drainage ditches bordering fields just south of the village of Santiago. Two females were found on dense masses of leaves above the ditches. Mueses-Cisneros (2005) provided much additional information on the occurrence of this species in the Valle de Sibundoy.

Estupiñán (2004) implied that *Gastrotheca ruizi* is an arboreal forest inhabitant, but Mueses-Cisneros (2005: 306) stated: “Contrary to Estupiñán (2004), the species is not arboreal, because the vegetation existing on the borders of water where *G. ruizi* lives is made up of herbs and small bushes, not trees” [translated from Spanish].

Conservation Status

Gastrotheca ruizi is listed as Endangered in the IUCN Red List, because of the small known range of its distribution in a region devoted to agriculture. Estupiñán (2004) suggested that the species might occur in a protected area, the Parque Nacional Natural Alto Fragua Indi Wasi, but the frog is not known to occur in the immediate vicinity of the park. Because the species is reasonably common in agricultural areas in the valley, Mueses-Cisneros (2005) suggested that *G. ruizi* should be categorized as Threatened. Pérez Villota and Duellman (2012) stated that the species is abundant in the Valle de Sibundoy, and therefore might be listed as being of Least Concern. Nonetheless, they recommended that the species be categorized as Vulnerable, because changes, such as the use of chemical herbicides, might be detrimental to the existence of the species in the small valley.

Etymology

The specific name *ruizi* is a patronym for the late Pedro M. Ruíz-Carranza of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, in Bogotá (Duellman and Burrowes, 1986).

Remarks

Analyses of molecular data reveal that *Gastrotheca aureomaculata* and *G. ruizi* are sister species in the northern clade of the subgenus *Duellmania*. Both species produce tadpoles that may require more than 100 days to complete their development.

Gastrotheca (*Duellmania*) *trachyceps* Duellman, 1987

Gastrotheca trachyceps Duellman, 1987.—Holotype: KU 144123, an adult female from Cerro Munchique on the road to the Pacific coast from El Tambo, 2170 m (02°28′ N, 77°01′ W), Departamento de Cauca, Colombia.

Diagnosis

This medium-sized species attains a maximum snout–vent length of 67.9 mm. The tibia length is less than 55% of the snout–vent length, and is slightly longer than the foot. The interorbital distance is about twice the width of the upper eyelid. The skin on the dorsum is smooth, adherent to, and partially co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first and second fingers are equal in length. The discs on the fingers are much wider than the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is green, with broad dark paravertebral marks. Markings on the head are restricted to a pale labial stripe in some individuals. A pale dorsolateral stripe is present. The flanks are brown or green; posteriorly they are blue, with black spots. The venter is creamy gray, with dark flecks.

In coloration, *Gastrotheca trachyceps* is similar to *G. argenteovirens* and *G. dunni*, but it differs from both by having the skin co-ossified with the dermal elements of the skull. Of other species having co-ossified skulls, the much larger *G. fissipes*, *megacephala*, *recava*, and *prasina* have broad skulls, with all the dermal roofing bones co-ossified with the overlying skin. In the much larger *G. nicefori* and *G. ovifera*, there is an elevated transverse occipital ridge. *G. weinlandii* also is much larger, has a prominent supratympanic ridge, and has a tan dorsum, with diagonal brown streaks extending onto the flanks. *G. galeata* differs by having the maxillae and premaxillae flared, thereby giving the skull a spatulate appearance.

Description

The following description is based on 14 specimens. The body is moderately robust. The maximum snout–vent length is 50.0 mm in males, and 67.9 mm in females. The head is slightly wider than long, and about as wide as the body. The snout is bluntly rounded in dorsal view, and is truncate in profile. The canthus rostralis is angular in cross-section. The loreal region is barely concave; the lips are slightly flared. The top of the head is slightly concave. The interorbital distance is about 200% of the width of the upper eyelid. The internarial area is flat. The nostrils are slightly protuberant, and are directed laterally at a point below the anterior terminus of the canthus rostralis and slightly posterior to the level of the anterior margin of the lower jaw. The diameter of the eye is about equal to its distance from the nostril. The tympanum is vertically ovoid, and is separated from the eye by a distance of about twice the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately heavy, tuberculate, extends from the posterior corner of the orbit to a point above the insertion of the arm, and obscures the upper edge of the tympanum.

The arm is moderately slender, and bears a row of low subconical ulnar tubercles. The hand is moderate in size. The fingers are moderately long, and bear round discs; the width of the disc on the third finger is about equal to the length of the tympanum. The relative lengths of the fingers are I = II < IV < III. The fingers are unwebbed. The subarticular tubercles are moderately large and low; the distal tubercle on the fourth finger is weakly bifid in some specimens. The supernumerary tubercles are small, subconical, and in a single row on the proximal segments of the digits (except the thumb). The palmar tubercle is low and weakly bifid; the prepollical tubercle is broad and ovoid; nuptial excrescences are absent. The hind limb is moderately slender. The tibia length is about 50% of the snout–vent length; the foot length is about 47% of the snout–vent length. Calcars, tarsal tubercles, and tarsal folds are absent. The outer metatarsal tubercle is minute and ovoid; the inner metatarsal tubercle is low, flat, elliptical, and barely visible from above. The toes are long. The relative lengths of the toes are I < II < III < V < IV. The toes are about one-third webbed; the webbing formula is **I**2—2^{+}**II**2^{-}—3^{+}**III**2—3^{+}**IV**3^{-}—(2–2½)**V**. The subarticular tubercles are moderately small and subconical; the supernumerary tubercles are small, and are few in number on the proximal segments of the digits.

The skin on the dorsal surfaces of the body and limbs and on the flanks is smooth; the skin in the loreal and postorbital regions and on the dorsum of the head is co-ossified with the underlying cranial elements; the skin on the throat, belly, and posteroventral surfaces of the thighs is weakly granular; the other ventral surfaces are smooth. A row of small tubercles is incorporated into the supratympanic fold, which extends posteriorly to the groin. Cloacal tubercles and folds are absent. The opening of the brood pouch is U-shaped, with the anterior border at the level of the sacrum. The dentigerous processes of the vomers are posteromedially inclined, and are narrowly separated medially between the small round choanae. Each process bears five to eight teeth.

Color in preservative

The dorsum of the head, forelimbs, shanks, and loreal region are bluish gray. On the dorsum of the body, irregular narrow paravertebral dark brown marks originate on the occiput, and extend to the postsacral region in 77% of the specimens. Scattered dark brown to black flecks are present on the dorsum in 85%. The postorbital region, flanks, and dorsal surfaces of the thighs are brown. A narrow creamy white dorsolateral stripe originates on the tip of the snout, then passes along the canthus rostralis, the outer edge of the upper eyelid, and the supratympanic fold, and extends to the groin. A pale rostral stripe connects the dorsolateral stripes with the labial stripes, which are expanded below the orbit and continuous above the insertion of the arm for about two-thirds the length of the flank. A cream-colored supracloacal stripe is present in 84%. A cream-colored heel stripe continues on the outer edge of the tarsus to the base of the disc on the fifth toe. The axilla is blue; the groin, anterior and posterior surfaces of the thighs, ventral surfaces of the shanks, and inner surfaces of the feet are blue, with dark grayish-brown or black spots and mottling. The throat, belly, and ventral surfaces of the thighs are creamy gray, with scattered black flecks.

COLOR IN LIFE

KU 181188–93 from Cerro Munchique, Departamento de Cauca, Colombia,—The dorsum is tan to reddish brown, with or without faintly darker paravertebral marks (Fig. 11.29); there is a greenish suffusion in KU 181189. The flanks are colored like the dorsum. The dorsolateral stripe is orange tan to bronze; the labial stripe is bronze. The venter is grayish tan, with dark brown to dark gray mottling. The axilla, groin, anterior and posterior surfaces of the thighs, and inner surfaces of the shanks and feet are predominately black, with dark blue mottling and yellow to orange spots. The palmar and plantar surfaces are dull bluish gray. The iris is dull grayish bronze, with fine black reticulations (W. E. Duellman field notes, 23 March 1979).

A brooding female (UMMZ 128837), also from Cerro Munchique.—This specimen has a bronze-tan dorsum, with brown paravertebral markings. The flanks are bronze, with dark brown flecks and a greenish tint ventrally. The axilla, groin, anterior surfaces of the thighs, and ventral surfaces of the shanks are mottled cream and bluish black. The dorsolateral and labial stripes are dull cream. The postorbital mark is brown. The iris is dull bronze, with black flecks (photo by K. Adler).

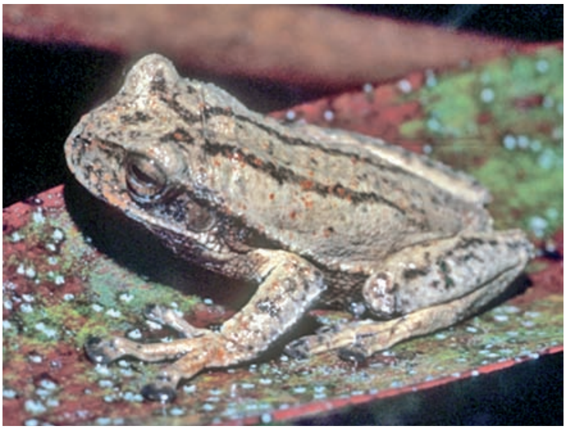

Fig. 11.29 *Gastrotheca trachyceps* (KU 118190), female, 55.5 mm SVL, W slope Cerro Munchique, Cauca, Colombia. Photo by W. E. Duellman.

MEASUREMENTS

The largest females are considerably larger than the only known adult male (Table 11.16).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous fine pit-and-ridge pattern. The nasals articulate medially, and are fused to one another; owing to synostosis, the posteromedial borders of the nasals are indistinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; each bears a wide supraorbital flange and a small otic flange. A temporal arcade is absent. The frontoparietal covers only the anterior epiotic eminence, and is partially fused to it; thus the carotid canal partially open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla,

Table 11.16 Univariate statistics for adults of *Gastrotheca trachyceps*

	Male ($n = 1$)	Females ($n = 13$)		
Character	Mean	Mean	Range	SD
Snout–vent length	50.0	54.1	40.2–67.9	8.60
Tibia length	24.3	27.4	20.6–33.4	4.19
Foot length	22.2	25.8	18.3–32.3	4.30
Head length	16.7	17.7	14.1–21.5	2.39
Head width	18.2	19.4	14.8–23.0	2.85
Interorbital distance	6.4	6.6	4.7–8.6	1.17
Eyelid width	4.0	3.8	2.5–4.7	0.61
Internarial distance	3.4	3.4	2.4–4.2	0.52
Eye diameter	5.0	4.8	4.0–5.7	0.52
Eye–nostril distance	5.2	5.0	2.8–6.1	0.90
Orbit–jaw distance	2.3	2.4	1.8–3.2	0.43
Nostril–jaw distance	3.8	3.8	2.6–5.1	0.74
Tympanum diameter	3.0	3.0	2.2–3.8	0.51
Thumb length	8.4	10.16	6.7–12.6	1.91
Third finger length	15.7	18.3	13.2–22.7	3.04
Disc width	2.6	3.2	2.0–4.0	0.65

which articulates with the dorsally adjacent nasal for only about one-fourth the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is long. The postorbital process of the maxilla is massive, and has a broad horizontal articulation with the wide zygomatic process of the squamosal. The head of the squamosal bears a narrow crest; the otic plate articulates with and narrowly overlaps the crista parotica. The dorsal part of the stapedial footplate is more than three times the length of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has a blunt terminus anterior to the level of the neopalatines. The sphenethmoid is ossified posterior to the midlength of the orbit, but is not synostosed with the prootic. The neopalatines are widely separated medially, and bear a ventral flange. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a long acuminate recurved process on the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located between the middle quadrants of the choanae.

Life History

A female (UMMZ 128837), having a snout–vent length of 67.9 mm, contained 47 eggs, 5.3 mm in diameter each, in the pouch. Another female (KU 144122), having a snout–vent length of 63.8 mm, was collected on 24 April 1971 and produced 13 tadpoles in Stage 37 on 9 May; nine partially developed eggs, having diameters of 5.6 mm each, were retained in the pouch. Six of the tadpoles metamorphosed on 6 June; the recently metamorphosed young (KU 148192) have snout–vent lengths of 17.4–20.5 mm ($\bar{x} = 19.0$).

Tadpoles

A hatchling tadpole (KU 148491) in Stage 37 has a body length of 11.6 mm, and a total length of 29.2 mm. In dorsal view the body is ovoid, widest at about two-thirds the length of the body, and has a rounded snout. In profile the body is highest at about three-fourths the length of the body, and is not as high as wide; the snout is inclined gradually from the nostrils to a rounded tip. The throat is concave. The eyes are small, and are directed dorsolaterally. The interorbital distance is slightly less than one-third the width of the body at the level of the orbits. The nostrils are directed anterolaterally, midway between the eyes and the tip of the snout. The spiracular tube short and sinistral, with a U-shaped opening directed posterodorsally on the ventrolateral surface at about 60% of the length of the body. The cloacal tube is moderately long, conical, and median, with a transverse opening. The caudal musculature is moderately robust; its height is slightly less than that of the dorsal fin at midlength of the tail. The musculature terminates gradually in a pointed tip well within the margin of the caudal fin. The dorsal fin arises gradually from the posterior edge of the body. The dorsal and ventral fins are about equal in height, and terminate in an acutely rounded tip.

The width of the oral disc is equal to about one-half the width of the body. The disc is bordered laterally and ventrally by two alternating rows of small blunt marginal papillae. There are two upper and three lower rows of labial teeth; the rows are about equal in length; the first lower row is narrowly interrupted medially. The upper jaw sheath is moderately slender, in the form of a continuous broad arch; the lower sheath is broadly V-shaped. Both sheaths bear fine serrations.

In preservative the body is brown; the caudal musculature is cream; the fins are translucent, with minute dark flecks. In life the body is greenish brown with small black flecks dorsally, transparent with a greenish tint laterally, and grayish yellow ventrally. The caudal musculature and hind limbs are creamy white to pale green, with black flecks; the fins are translucent, with a greenish tint.

Advertisement Call

The call consists of a long "wraack," followed by two or three shorter notes, "tlok, tlok." No recordings are available.

Distribution and Ecology

Gastrotheca trachyceps is known only from elevations of 2170–2540 m on the Pacific slopes of Cerro Munchique in the Cordillera Occidental in southern Colombia (Fig. 11.3). Individuals were found in and heard calling from large terrestrial bromeliads by day.

Conservation Status

Gastrotheca trachyceps is categorized as Endangered in the IUCN Red List, both because of its small geographic range and because there is continuing decline in the extent and quality of its habitat on the Cordillera Occidental.

Etymology

The specific name is derived from the Greek *trachy*, meaning "rough," and the Greek *ceps*, meaning "head"; it was applied to this species because of the rough appearance of the head, in which the skin is co-ossified with the underlying skull bones (Duellman, 1987).

Remarks

Although *Gastrotheca trachyceps* is morphometrically like *G. argenteovirens* in the Cordillera Central of Colombia (Duellman, 1987), the species differ in that adults of *G. trachyceps* have the skin co-ossified with the skull. Analyses of molecular data show that these two taxa are sister species within a small clade that also includes *G. aureomaculata*, *dunni*, and *ruizi*, all confined to the Andes in Colombia.

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12

Andean Species of Subgenus *Gastrotheca*

This chapter is an account of the second major clade of Andean *Gastrotheca*.

Subgenus *Gastrotheca* Fitzinger, 1843

Gastrotheca Fitzinger, 1843:30. Type species—*Hyla marsupiata* Duméril and Bibron, 1841, by original designation.

Definition

Most members of the subgenus *Gastrotheca* are medium-sized frogs, but *G. carinaceps* and *G. testudinea* are large. The skin on the head is not co-ossified with the underlying dermal bones, except in three species (*G. ossilaginis*, *splendens*, and *testudinea*). The range in the snout–vent lengths in adults is 27–61 mm in males, and 32–68 mm in females; exceptions are *G. carinaceps* and *G. testudinea*, with maximum snout–vent lengths of 79.7 and 82.6 mm, respectively. The mean percentage of tibia length to snout–vent length is 46.6%; only seven species exceed 50%. The head is wider than long (head width 31.5%–43.8% of snout–vent length, and head length 29.7%–34.8% of snout–vent length). All species lack dermal ornamentation. The dorsum is green or brown, usually with either a darker middorsal blotch or paravertebral marks.

Among the osteological features of this subgenus are a semicoarse pit-and-ridge pattern of dermal sculpturing on the skull table, and a tendency for a reduction in cranial ossification. A group of species roughly corresponding to the Peruvian clade (Fig. 12.1) has a variety of plesiomorphic characters, such as lacking a supraorbital flange on the frontoparietal and having small nasals that do not articulate medially. A group of species in the southern clade also have reduced cranial ossification (see chapter 4 for details).

Reproduction

Twelve of the species are known to produce eggs that hatch as free-swimming feeding tadpoles, whereas the majority of the taxa have eggs that undergo direct development.

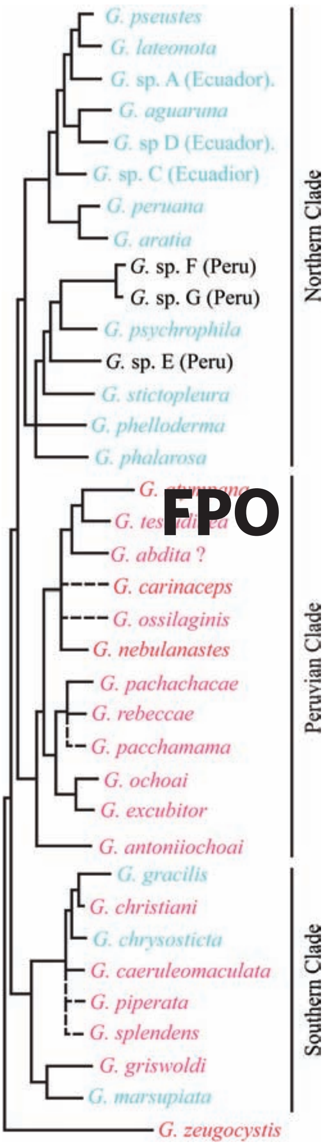
G. pseustes
G. lateonota
G. sp. A (Ecuador).
G. aguaruma
G. sp D (Ecuador).
G. sp. C (Ecuadior)
G. peruana
G. aratia
G. sp. F (Peru)
G. sp. G (Peru)
G. psychrophila
G. sp. E (Peru)
G. stictopleura
G. phelloderma
G. phalarosa
Northern Clade
FPO
G. abdita ?
G. carinaceps
G. ossilaginis
G. nebulanastes
G. pachachacae
G. rebeccae
G. pacchamama
G. ochoai
G. excubitor
G. antoniiochoai
Peruvian Clade
G. gracilis
G. christiani
G. chrysosticta
G. caeruleomaculata
G. piperata
G. splendens
G. griswoldi
G. marsupiata
Southern Clade
G. zeugocystis

Fig. 12.1 Hypothesized phylogenetic relationships among species of the subgenus *Gastrotheca*, based on molecular data. Species lacking molecular data are tentatively placed (dashed lines), based on morphological synapomorphies. Species names in blue have feeding tadpoles; those in red undergo direct development; for those in black, the reproductive mode is unknown.

Distribution

Species in this subgenus occur in the Andes from central Ecuador to Bolivia, with a hiatus between those and species in northwestern Argentina. Most of the species occur at elevations in excess of 2500 m, and three (*Gastrotheca marsupiata*, *peruana*, and *pseustes*) extend to elevations in excess of 4000 m.

Content

Twenty-nine species, plus at least six undescribed species.

Etymology

The generic name is derived from the Greek *gastros*, meaning "belly," and the Greek *theke*, meaning "container"; Fitzinger (1843), who coined the name, may have thought that the brood pouch was on the venter.

Remarks

Three major clades exist within this subgenus (Fig. 12.1). The northernmost of these clades ranges from central Ecuador to central Peru; all species in this clade whose mode of life history is known produce eggs that hatch as tadpoles. The Peruvian clade is restricted to the Cordillera Central and Cordillera Oriental in Peru; all species in that clade have direct development. The southern clade ranges from central Peru to northwestern Argentina; three species therein have tadpoles, and five have direct development. Basal to these three clades is *Gastrotheca zeugocystis*, which has direct development. Therefore tadpoles are derived at the root of the northern clade, whereas direct development is basal in the Peruvian and southern clades. Within the southern clade, tadpoles have evolved twice: *G. chrysosticta-gracilis* and *G. marsupiata*. In the former lineage, a reversal led to direct development in *G. christiani*. A great plasticity seems to exist in the reproductive mode in subgenus *Gastrotheca*.

KEY TO SPECIES OF *GASTROTHECA*

1. Skin on head co-ossified with or adherent to skull 2
Skin on head not co-ossified with or adherent to skull 4

2. Skin on head adherent to skull; Finger I longer than Finger II; inner tarsal fold present on distal one-third of tarsus .... *G. testudinea*
Skin on head co-ossified with skull; Finger I not longer than Finger II; inner tarsal fold absent 3

3. Snout truncate in dorsal view, and inclined anteroventrally in profile; webbing on foot basal ....*G. ossilaginis*
Snout bluntly rounded in dorsal view and in profile; webbing on foot extending to antepenultimate subarticular tubercle on Toe IV and point between antepenultimate and penultimate subarticular tubercles on Toe V .... *G. splendens*

4. Skin on dorsum pustular.. 5
Skin on dorsum smooth, shagreen, or granular............ 7

5. Venter black, with white spots; inner tarsal fold present on distal one-fifth of tarsus .... *G. phalarosa*
Venter pale; inner tarsal fold extending full length of tarsus 6

6. Dorsum bearing prominent longitudinal pustular ridges .... *G. phelloderma*
Dorsum bearing round or elliptical pustules .... *G. peruana*

7. Tympanum absent .... *G. atympana*
Tympanum present 8

8. Small tubercle on heel .... *G. abdita*
No tubercle on heel 9

9. Inner tarsal fold extending full length of tarsus 10
Inner tarsal fold, if present, existing only on no more than distal half of tarsus 13

10. Tympanum round; canthus rostralis acutely rounded in cross-section 11
Tympanum vertically ovoid; canthus rostralis bluntly rounded in cross-section 12

11. Tympanic annulus granular; snout–vent length less than 50 mm .... *G. piperata*
Tympanic annulus smooth; snout–vent length more than 50 mm .... *G. aratia*

12. Large frogs; snout–vent length in females greater than 60 mm; snout slightly inclined anteroventrally in profile; flanks dark, with pale spots .... *G. stictopleura*
Small frogs; snout–vent length in females less than 40 mm; snout bluntly rounded in profile; flanks uniformly colored .... *G. pacchamama*

13. Webbing basal between Toes III, IV, and V 14
Webbing extending at least to antepenultimate subarticular tubercles on Toes III, IV, and V 16

14. Finger I longer than Finger II; interorbital distance much greater than width of upper eyelid; skin on dorsum distinctly granular .... *G. nebulanastes*
Finger I shorter than or equal to Finger II; interorbital distance no more than slightly greater than width of upper eyelid; skin on dorsum not granular 15

15. Snout in dorsal view broadly rounded, in profile truncate; skin on dorsum shagreen .... *G. antoniiochoai*
Snout in dorsal view acuminate, in profile rounded; skin on dorsum smooth .... *G. zeugocystis*

16. Disc on third finger much wider than distal part of digit 17
Disc on third finger only slightly wider than distal part of digit 24

17. Cranial crests present; tibia length greater than 55% of snout–vent length; dorsum uniformly green .... *G. carinaceps*
Cranial crests absent; tibia length less than 55% of snout–vent length; dorsal coloration variable 18

18. Snout in profile truncate .... *G. chrysosticta*
Snout in profile bluntly rounded or inclined anteroventrally 19

19. Outer fingers webbed basally 20
Webbing absent between fingers 21

20. Skin on dorsum tuberculate .... *G. christiani*
Skin on dorsum smooth or areolate .... *G. psychrophila*

21. Dark brown canthal stripe and interorbital bar present; pale dorsolateral stripe usually present .... *G. rebeccae*
Dark brown canthal stripe, brown interorbital bars, and pale dorsolateral stripe absent .... *G. ochoai*

22. Inner tarsal fold absent 22
Inner tarsal fold present distally on tarsus 23

23. Skin on dorsum smooth; in life blue spots present on flanks and dorsum .... *G. caeruleomaculata*
Skin on dorsum granular; color not as described .... *G. pachachacae*

24. Basal webbing between Fingers III and IV; skin on dorsum with low flat tubercles .... *G. gracilis*
No webbing between Fingers III and IV; skin on dorsum not as described 25

25. Finger I longer than Finger II .... *G. aguaruna*
Finger I shorter than or equal in length to Finger II 26

26. Interorbital distance about twice width of upper eyelid; tympanic annulus granular .... *G. excubitor*
Interorbital distance only slightly greater than width of upper eyelid; tympanic annulus smooth 27

27. Large frogs; snout–vent length more than 50 mm in adults; tympanum vertically ovoid .... *G. pseustes*
Small frogs; snout–vent length less than 50 mm; tympanum round 28

28. Interorbital bar not connected to markings on dorsum of body .... *G. marsupiata*
Interorbital bar with median connection to dorsal markings on body .... *G. griswoldi*

Gastrotheca (*Gastrotheca*) *abdita* Duellman

Gastrotheca abdita Duellman, 1987:903.—Holotype: KU 196833 from the Cordillera Colán, E La Peca, 2970 m, Región de Amazonas, Peru.

Diagnosis

In this moderately small species, the tibia length is less than 50% of the snout–vent length; the tibia is about as long as the foot. The interorbital distance is about twice the width of the eyelid. The skin on the dorsum is smooth, not co-ossified with the skull, and lacks transverse granular ridges. Supraciliary processes are absent. The heel bears a small conical tubercle; the tympanic annulus is tubercular. The first and second fingers are equal in length. The discs on the fingers are much wider than the adjacent digits. The fingers lack webbing; on the toes the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is tan, with a narrow brown middorsal mark anteriorly, which bifurcates posteriorly. Markings on the head consist of a dark labial stripe; a pale dorsolateral stripe is absent. The flanks are uniformly dark brown; the venter is uniformly pale tan.

Gastrotheca abdita differs from all other named *Gastrotheca* (except *G. ochoai*) in the Peruvian Andes by having an acuminate snout in dorsal view. *G. ochoai* differs from *G. abdita* by having scattered tubercles on the dorsum, dark canthal and supratympanic stripes, less webbing on the foot, and no tarsal fold. The other species of *Gastrotheca* in the high Andes of Peru with direct development have rounded snouts, and *G. galeata* has a casqued co-ossified head.

Description

The following description is based on one adult male and nine adult females. The body is moderately robust; the maximum snout–vent length is 36.0 mm in males, and 46.2 mm in females. The head is slightly wider than long. The snout is subacuminate in dorsal view, and is bluntly rounded in profile. The canthus rostralis is angular in cross-section. The loreal region is slightly concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 200% of the width of the upper eyelid. The internarial area is flat. The nostrils are slightly protuberant, directed laterally at a point slightly posterior to the anterior margin of the lower jaw below the anterior terminus of the canthus rostralis. The diameter of the eye is slightly greater than its distance from the nostril. The tympanum is vertically ovoid, separated from the eye by a distance half again the length of the tympanum. The tympanic annulus is distinct and tuberculate. The supratympanic fold is moderately heavy, tuberculate, extends from the posterior corner of the eye to a point above the insertion of the arm, and obscures the upper part of the tympanum.

The arm is moderately robust; a row of low conical ulnar tubercles is present. The hand is moderate in size. The fingers are unwebbed. The discs on the fingers are large and round; the diameter of the disc on the third finger is equal to the length of the tympanum. The relative lengths of the fingers are I = II < IV < III. The subarticular tubercles are large and subconical; the outer tubercle on the fourth finger is distinctly bifid. The supernumerary tubercles are moderately large, subconical, and numerous on the proximal segments of the fingers. The palmar tubercle is large and distinctly bifid; the prepollical tubercle is elongate and ovoid; in males it bears black nuptial excresences. The hind limbs are moderately slender. The tibia length is 45.0%–52.4% ($\bar{x} = 48.6$) of the snout–vent length; the foot length is 42.6%–51.4% ($\bar{x} = 47.9$) of the snout–vent length. The heel bears a small subconical tubercle; the inner tarsal fold is distinct on the distal two-thirds of the tarsus. The outer metatarsal tubercle is small and round; the inner metatarsal tubercle is elevated, elongate, and visible from above. The toes are rather short. The relative lengths of the toes are I < II < III = V < IV. The toes are about one-fourth webbed; the webbing formula is **I**2—2**II**2—(3$^-$–3)**III**(3$^-$–3)—(3–3$^+$)**IV**(3–3$^+$)—2**V**. The subarticular tubercles are moderately large and subconical; the supernumerary tubercles are small, subconical, and present only on the proximal segments of the toes.

The skin on the dorsum is smooth, with small tubercles on the supratympanic fold and the side of head posterior to the eye. The skin on the flanks, belly, and proximal posteroventral surfaces of the thighs is granular. Cloacal tubercles and folds are absent. The opening of the brood pouch is narrowly U-shaped, with the anterior border at the level of the sacrum. The dentigerous processes of the vomers are posteromedially inclined, narrowly separated medially, slightly posterior to small the round choanae, and bear six or seven teeth.

COLOR IN PRESERVATIVE

The dorsum is dull grayish brown, with a darker brown middorsal mark beginning on the top of the head or in

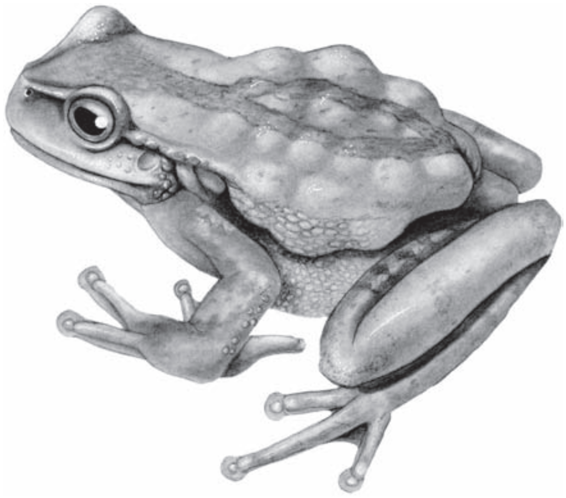

Fig. 12.2 *Gastrotheca abdita* (KU 196833, holotype), female, 44.6 mm SVL, Cordillera Colán, Amazonas, Peru. Drawing by Gretchen Bracher.

Table 12.1 Univariate statistics for adults of *Gastrotheca abdita*

	Male ($n = 1$)	Females ($n = 9$)		
Character	Mean	Mean	Range	SD
Snout–vent length	36.0	43.0	38.0–46.2	2.60
Tibia length	16.4	21.0	19.2–22.4	1.15
Foot length	16.4	20.7	16.2–22.8	2.12
Head length	12.5	14.5	13.4–15.3	0.69
Head width	13.8	16.2	14.6–17.4	1.12
Interorbital distance	4.4	5.4	4.8–6.1	0.41
Eyelid width	3.0	3.0	2.6–3.3	0.28
Internarial distance	2.2	2.7	2.4–2.9	0.16
Eye diameter	3.7	4.1	3.6–4.6	0.35
Eye–nostril distance	3.4	3.8	3.0–4.3	0.39
Orbit–jaw distance	2.2	2.3	1.9–2.6	0.27
Nostril–jaw distance	2.6	3.3	2.9–3.9	0.33
Tympanum diameter	2.1	2.3	2.1–2.4	0.11
Thumb length	6.0	7.6	6.0–8.5	0.81
Third finger length	11.0	13.7	11.7–15.2	1.25
Disc width	1.9	2.4	1.7–3.0	0.44

the occipital region, bifurcating just posterior to the scapula, and coalescing just anterior to its terminus at the anterior border of the pouch. There are scattered dark flecks on the dorsum, and faint narrow transverse marks on the thighs, shanks, and feet. The flanks and anterior surfaces of the thighs are dull brown; the posterior surfaces of the thighs are pale brown, with a few darker flecks; the venter is uniformly dull tan. Canthal, labial, dorsolateral, and supracloacal stripes are absent (Fig. 12.2).

COLOR IN LIFE

Notes by L. J. Barkley accompanying four specimens indicate that two were green, one was pale brown, and one was green, brown, and red.

MEASUREMENTS

The only known male has a snout–vent length of 36.0 mm. Nine adult females have snout–vent lengths of 38.0–46.2 mm ($\bar{x} = 43.0$) (Table 12.1).

CRANIAL OSTEOLOGY

The dermal roofing bones are not co-ossified with the overlying skin; the sphenethmoid is sculptured. The nasals articulate medially; their borders are not distinct from the sphenethmoid. The frontoparietals articulate medially throughout their lengths; each frontoparietal bears a moderately wide supraorbital flange, and has an otic flange not articulating with the squamosal. A temporal arcade is absent. The carotid canal is enclosed. The preorbital process is not separated by a notch from the facial process of the maxilla; a postorbital process is present on the maxilla. The head of the squamosal has a narrow crest; the zygomatic ramus extends to the maxilla; the otic ramus completely articulates with and moderately overlaps the ossified crista paroticae. An auxiliary dorsal ramus of the squamosal is absent. The parasphenoid has a short posteromedian process; the cultriform process terminates posterior to the level of the neopalatines; the parasphenoid alae articulate with the pterygoids. The neopalatines are moderately separated medially and do not form the posterior margin of the choanae; ventral ridges are present on the neopalatines. The pterygoids articulate with the squamosals; the median ramus of the pterygoid is not expanded medially; an auxiliary dorsal ramus is present.

Life History

Eight brooding females contained 12–21 embryos ($\bar{x} = 15$) that develop directly into froglets. These specimens were collected on 30 August–7 September 1978.

Advertisement Call

The call is unknown.

Distribution and Ecology

This species is known only from the higher western slopes of the Cordillera Colán in the Huancabamba

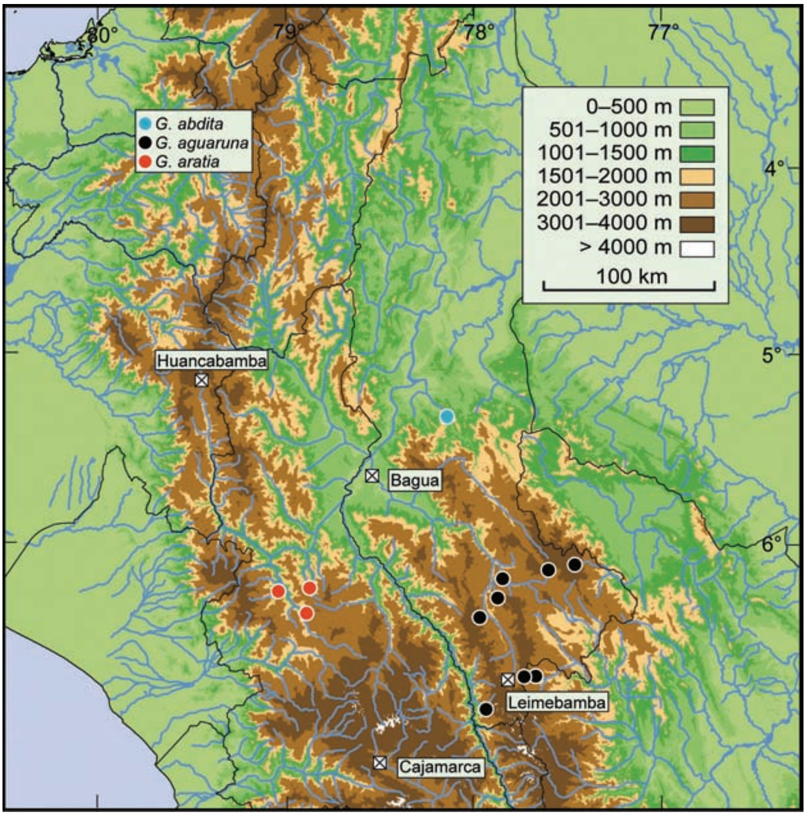

Fig. 12.3 Andean region of southern Ecuador and northern Peru, showing the localities of known occurrences of *Gastrotheca abdita*, *aguaruna*, and *aratia*.

Depression in northern Peru (Fig. 12.3). The frogs were found above treeline at elevations of 2970–3330 m. Brooding females were found in grassy areas, in a bog, and on the fronds of a spiny terrestrial bromeliad.

Conservation Status

The species is listed as Data Deficient in the IUCN Red List.

Etymology

The specific name is derived from the Latin verb *abdo*, meaning "to remove" or "to exile," and was used in reference to the geographic isolation of the Cordillera Colán, the only known region inhabited by these frogs (Duellman, 1987).

Remarks

Gastrotheca abdita seems to be most closely related to other small high-Andean species in Peru that have direct development—*G. excubitor*, *griswoldi*, *pacchamama*, and *rebeccae*—but it is widely separated geographically from those species, all of which occur in the Andes of central and southern Peru. The questioned *G. abdita* in the molecular phylogeny is based on tissue collected by P. J. Venegas in the Cordillera Colán, where *G. abdita* is the only species of the genus known. I have not seen the specimen.

Gastrotheca (*Gastrotheca*) *aguaruna* Duellman, Barley, and Venegas

Gastrotheca aguaruna Duellman, Barley, and Venegas, 2014: 164.—Holotype: KU 212022 from Molinopampa, Región de Amazonas, Peru.

Diagnosis

Adults of this moderately large species attain a snout–vent length of 51 mm. The tibia length is about 50% of the snout–vent length, and is about as long as the foot. The interorbital distance is about equal to the width of the upper eyelid. The skin on the dorsum is weakly granular to smooth, not co-ossified with skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. Fingers I and II are equal in length. The discs on the fingers are slightly wider than the digits. The fingers are unwebbed; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and nearly to the penultimate subarticular tubercle on the fifth toe.

The dorsum is green, with or without faintly darker paravertebral marks. Markings on the head consist of a pale labial stripe and (in some individuals) a dark canthal stripe. A pale dorsolateral stripe is present or not. The flanks and anterior and posterior surfaces of the thighs lack dark markings; black spots or reticulations are present in the groin; the venter is cream, with or without faint dark flecks or spots.

Gastrotheca aguaruna most closely resembles four other species in northern Peru. In contrast to the much larger *G. monticola*, *G. aguaruna* lacks a pale supracloacal stripe and black spots on the flanks and anterior and posterior surfaces of the thighs. The slightly larger *G. aratia* differs from *G. aguaruna* by lacking black marks in the groin and by having slightly more webbing on the foot; the web extends to the penultimate subarticular tubercle of Toe IV. *G. dysprosita* differs from *G. aguaruna* by having a green dorsum with a narrow yellow middorsal stripe, and green flanks with small yellow spots; furthermore, *G. dysprosita* lacks a dark canthal stripe and a pale labial stripe. *G. lateonota* is like *G. monticola* in size and in most proportions, but *G. lateonota* differs from *G. monticola* and *G. aguaruna* by having a truncate snout in profile, smooth skin on the dorsum, and a nearly uniform grayish-brown venter. Six other species of *Gastrotheca* in the Andes are present in northern Peru. *G. peruana*, *phalarosa*, and *phelloderma* all have pustular skin on the dorsum. *G. aratia* differs from *G. aguaruna* by having a tarsal fold extending the full length of the tarsus, and by having no dark marks in the groin and on the hidden surfaces of the thighs; *G. abdita* differs by having an acuminate snout in dorsal view. *G. galeata* differs from all of the others by having a spatulate labium. The latter two species also produce eggs that undergo direct development, whereas *G. aguaruna* has eggs that hatch as tadpoles. The Ecuadorian *G. pseustes* differs from *G. aguaruna* by having coarsely granular skin on the dorsum, dark spots or flecks on a cream venter, and an anteroventrally inclined snout in profile.

Description

The following description is based on nine specimens. The body is robust; females are slightly larger than males, which attain snout–vent lengths of 50.8 mm and 46.8 mm, respectively. The head is as wide as long. The snout is rounded in dorsal view and in profile. extending slightly beyond the margin of the lower lip. The canthus rostralis is acutely rounded in cross-section. The loreal region is concave; the lips are rounded. The top of the head is flat. The interorbital distance is equal to the width of the upper eyelid. The internarial area is flat. The nostrils are not protuberant, and are located near the terminus of the canthus rostralis posterior to the level of the anterior margin of the lower jaw. The diameter of the eye is much greater than its distance from the nostril. The tympanum is round, and is separated from the eye by a distance about 1.5 times the length of the tympanum. The tympanic annulus is weak and smooth. The supratympanic fold is moderately heavy; it extends from the posterior corner of the orbit to a point posterior to the tympanum, and obscures the upper edge of the tympanum.

The arm is robust; ulnar tubercles are absent. The hand is moderately large. The fingers are short and unwebbed. The terminal discs are small, rounded, and slightly wider than the digits proximal to the disc; the width of the disc on the third finger is equal to about half the length of the tympanum. The relative lengths of the fingers are I > II < IV < III. The subarticular tubercles are low and rounded; none are bifid. The supernumerary tubercles are small, and are present only on the proximal segments of the digits. The palmar tubercle is absent; the prepollical tubercle is elongate; breeding males have small brown nuptial excrescences on the medial surface of the thumb. The hind limb is robust. The mean ratio of tibia length and foot length to snout–vent length is 49%. Calcars and tarsal tubercles are absent. An inner tarsal fold is prominent on the distal half of the tarsus. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is large, elliptical, and barely visible from above. The toes are long. The relative lengths of the toes are I < II < III < V < IV. The webbing is basal between Toes I and II; the webbing formula for the other toes is **II**1—2**III**1½—2**IV**2—1**V**. The subarticular tubercles are small and rounded. Supernumerary tubercles are present only on the proximal segments of the digits.

The skin on the dorsum and flanks is weakly granular to smooth; the skin on the throat, belly, and ventral surfaces of the thighs is granular; the other surfaces are smooth. Cloacal tubercles and folds are absent. The opening of the brood pouch is puckered. The dentigerous processes of the vomers are inclined posteromedially, and are narrowly separated medially between the round choanae. Each process bears four to six teeth.

COLOR IN PRESERVATIVE

The dorsal surfaces of the head, body, and limbs are gray. A pair of slightly darker paravertebral marks is barely discernible in some specimens. The flanks are dull brown; the groin is gray, with irregular black markings. A fragmented faint pale gray dorsolateral

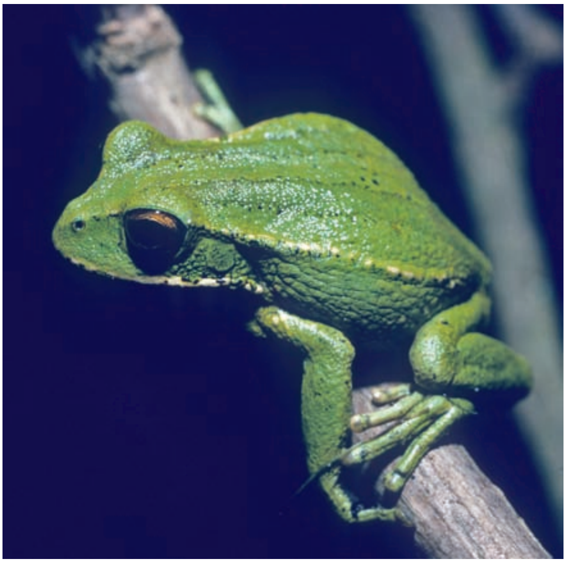

Fig. 12.4 *Gastrotheca aguaruna* (KU 212024), male, 44.0 mm SVL, Molinopampa, Amazonas, Peru. Photo by W. E. Duellman.

stripe is bordered below by a fragmented narrow black stripe; these stripes extend from the thoracic region and the groin. A dark brown canthal stripe is present; a white labial stripe borders either part of or the entire margin of the upper lip, and extends posteriorly to the base of the forelimb. The posterior surfaces of the thighs are gray, with faintly darker irregular markings. All ventral surfaces are dull tan, with small gray spots on the throat and chest.

COLOR IN LIFE

The basic dorsal color is green, with or without creamy yellow labial and dorsolateral stripes. The dorsum itself is green, with or without faintly distinct darker green or brown paravertebral marks (Fig. 12.4). The paravertebral marks may be absent, or represented by a faint outline. In some specimens the paravertebral marks are a green that is barely darker than the ground color, whereas distinct brown paravertebral marks are evident in others. Small black flecks are present on the dorsum in some individuals. There is a faint tinge of pale blue on the posterior surfaces of the thighs and in the groin, where small black marks are present; the venter is cream, with or without faint black spots. The vocal sac in calling males is pale green. The iris is copper colored.

MEASUREMENTS

Males are slightly smaller than females (Table 12.2).

CRANIAL OSTEOLOGY

No skeletal preparations are available.

Life History

The eggs hatch as tadpoles.

Tadpoles

Series of tadpoles and metamorphosing young were obtained at the type locality on 26 January 1989. A typical tadpole in Stage 39 (KU 212494) has a body length of 26.5 mm, and a total length of 66.4 mm. In dorsal view the body is ovoid, and is widest at midlength; the snout is bluntly rounded. In profile the body is highest posteriorly, and is gradually inclined to a rounded snout. The body is as wide as high. The throat is convex. The eyes are small, and are directed dorsolaterally. The interorbital distance is about one-third the width of the body at the level of the orbits. The nostrils are slightly closer to the eyes than to the tip of the snout. The spiracular tube is short, and is attached to the body throughout its length. The spiracular opening is directed posterolaterally on the ventrolateral surface of the body at a point about 55% of the length of the body. The cloacal tube is short, conical, and dextral, with a transverse opening. The caudal musculature is slender, and is not as high as the dorsal fin at midlength of the tail. The musculature terminates in a pointed tip just short of the margin of the caudal fin. The dorsal fin arises gradually from the proximal part of the caudal musculature. The height of the dorsal fin is slightly greater than that of the ventral fin at midlength of the tail; the fins terminate in a rounded tip.

The width of the oral disc is about one-third the width of the body. The disc is bordered laterally by a single row of short blunt marginal papillae, and ventrally by two rows of alternating papillae. There are two upper and three lower rows of labial teeth; the upper rows are slightly longer than the lower ones, and are subequal in length; the lower rows are progressively shorter; all rows are complete. The upper jaw sheath is slender, and is broadly arch-shaped; the lower sheath is more massive, and is broadly V-shaped. Both sheaths bear low blunt serrations.

In preservative the body is dull brown. The skin on the ventrolateral surfaces and on the venter is unpigmented. The caudal musculature is cream, with a brown streak along the upper edge. The fins are translucent, with fine brown reticulations. In life the body is olive tan; some tadpoles in advanced stages are greenish brown with brown paravertebral stripes, whereas

Table 12.2 Univariate statistics for adults of *Gastrotheca aguaruna* and *G. aratia*

		G. aguaruna (6 males, 3 females)			*G. aratia* (8 males, 1 female)		
Character	Sex	Mean	Range	SD	Mean	Range	SD
Snout–vent length	males	45.1	41.6–46.8	2.17*	48.1	42.8–55.7	4.6
	females	50.1	49.4–50.8	—	56.8	—	—
Tibia length	males	21.8	20.0–22.8	1.17*	22.4	19.7–27.7	2.72
	females	25.0	23.3–26.8	—	25.4	—	—
Foot length	males	22.0	20.1–24.0	1.39	22.4	20.1–26.3	2.33
	females	24.4	23.3–25.8	—	25.1	—	—
Head length	males	16.5	13.9–25.4	4.41	16.3	15.0–18.0	1.09
	females	15.8	14.8–16.6	—	18.8	—	—
Head width	males	17.4	14.8–26.4	4.43	16.8	14.6–19.0	1.54
	females	17.2	16.5–18.0	—	19.5	—	—
Interorbital distance	males	4.6	4.3–4.8	0.26	4.6	3.8–5.5	0.34
	females	5.1	5.0–5.3	—	5.3	—	—
Eyelid width	males	4.4	4.1–5.0	0.34	5.0	4.4–5.9	0.60
	females	5.0	4.9–5.0	—	6.3	—	—
Internarial distance	males	3.3	2.9–3.7	0.33	3.5	2.9–3.9	0.34
	females	2.9	2.7–3.1	—	3.4	—	—
Eye diameter	males	4.7	4.3–5.5	0.43***	5.5	5.0–5.9	0.31
	females	5.4	5.3–5.5	—	6.9	—	—
Eye–nostril distance	males	4.0	3.8–4.2	0.13	4.4	3.5–5.8	0.74
	females	4.7	4.1–5.0	—	5.0	—	—
Orbit–jaw distance	males	2.1	1.9–2.3	0.15**	2.3	2.2–2.4	0.10
	females	2.4	2.2–2.6	—	2.6	—	—
Nostril–jaw distance	males	3.1	2.7–3.7	0.35*	3.0	2.8–3.5	0.23
	females	3.9	3.8–4.0	—	4.1	—	—
Tympanum diameter	males	2.9	2.5–3.3	0.33**	3.6	3.1–4.5	0.49
	females	3.3	2.8–4.0	—	4.4	—	—
Thumb length	males	8.4	7.9–9.5	0.56*	9.0	8.0–10.4	1.03
	females	9.9	9.3–10.3	—	10.7	—	—
Third finger length	males	14.9	13.2–15.8	1.10*	15.5	13.5–18.5	1.92
	females	17.2	17.2–17.3	—	18.0	—	—
Disc width	males	1.7	1.5–1.9	0.14***	2.1	1.8–2.5	0.23
	females	2.3	2.2–2.3	—	2.2	—	—

*Differences between the means of the sexes in *G. aguaruna* significant (ANOVA, $P \leq 0.01$).

**Differences between the means for males of the two species are significant (ANOVA, $P \leq 0.01$).

***Differences between the means of the sexes in *G aguaruna* are significant, and differences between the means for the males of the two species are significant (ANOVA, $P \leq 0.01$).

others have cream dorsolateral stripes (W. E. Duellman field notes, 26 January 1989).

In the series of tadpoles from the type locality, the smallest is in Stage 29, with has a body length of 10.2 mm, and a total length of 24.0 mm. It has a full complement of tooth rows, and a brown streak on the dorsal edge of the caudal musculature. Several series of tadpoles from different localities in Región de Amazonas are like those from the type locality in structure and coloration, except that in some individuals the second upper and/or first lower tooth row is narrowly interrupted medially.

In a series of metamorphosing young from the type locality, 10 individuals with black pigment above the cloacal opening but no caudal protrusions have snout–vent lengths of 18.4–24.2 mm ($\bar{x} = 21.5 \pm 1.35$). The young were found in grasses and bushes alongside as well as on emergent vegetation in a slowly flowing marshy stream in pasture by day. The dorsum was either uniformly green, green with darker green or brown paravertebral marks, or tan with dark brown paravertebral marks; the venter was dirty white. The iris was copper-colored. (W. E. Duellman field notes, 26 January 1989).

Advertisement Call

The call consists of a low-pitched note, usually followed by two or three shorter notes. No recordings are available.

Distribution and Ecology

Gastrotheca aguaruna is known from elevations of 2360–3308 m in the northern part of the Cordillera Central in Peru (Fig. 12.3). The frogs have been found by day under clods of dirt in potato fields, on bushes and in emergent vegetation in a sluggish stream, and on leaves of bromeliads in grassy puna; gravid females were basking on the ground in puna. At night males have been observed calling from low bushes.

Conservation Status

The apparent abundance of this species in agricultural areas, as well as in high Andean regions not amenable to agriculture, suggest that *Gastrotheca aguaruna* should be categorized on the IUCN Red List as being of Least Concern.

Etymology

According to the original description (Duellman et al., 2014), the specific name *aguaruna* is a noun in apposition referring to the Aguaruna, the indigenous people of the Andes of northern Peru, including Región de Amazonas, where most specimens of the species have been collected.

Remarks

Gastrotheca aguaruna is most closely related to *G. lateonota* and *G. pseustes*, which, together with *G. aguaruna*, are the northernmost members of the central Andean clade of the genus.

Gastrotheca (*Gastrotheca*) *antoniiochoai* (De la Riva and Chaparro)

Hyla antoniiochoai De la Riva and Chaparro, 2005:516.—Holotype: MHNC 68 from near Quebrada Toqoryuoc, Wayqecha Research Center, Región de Cusco, Peru.

Gastrotheca antoniiochoai—Catenazzi and Lehr, 2009:63.

Diagnosis

This small species attains a maximum snout–vent length of 32.5 mm. The tibia length is 51.6% of the snout–vent length, and is slightly longer than the foot. The interorbital distance is less than the width of the upper eyelid. The skin on the dorsum is smooth to finely shagreen, not co-ossified with skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is shorter than the second. The discs on the fingers are slightly wider than the digits proximal to the discs. The fingers are unwebbed; webbing is absent on the foot, except for basal webbing between the third and fifth toes. The dorsum is brown to golden tan, with brown or green flecks. The only markings on the head are a dark brown canthal stripe and diffuse postorbital stripe. A pale dorsolateral stripe is absent. The flanks are tan; the venter is white to dull cream.

In the Andes of Bolivia and southern Peru, there are 11 small to moderately small species of *Gastrotheca* that have the first finger shorter than the second and small digital discs. Of these, *G. atympana* is unique in that it lacks a tympanum, and *G. splendens* is unique in having the skin co-ossified with underlying cranial elements. Only two species, *G. antoniiochoai* and *G. zeugocystis*, have paired lateral brood pouches; with the exception of *G. atympana*, which is known only from a male, all others (*G. excubitor*, *marsupiata*, *ochoai*, *pacchamama*, *pachachacae*, *piperata*, *rebeccae*, and *splendens*) have single dorsomedian brood pouches. The webbing on the feet is basal in *G. antoniiochoai* and *G. zeugocystis*, whereas the webbing extends at least to the antepenultimate subarticular tubercle on the fifth toe in all of the others. The tympanic annulus is smooth in most of the species, but it is granular in *G. excubitor* and some specimens of *G. piperata*. A dark interocular bar is present in most of the species, but it is absent in *G. antoniiochoai*, *ochoai*, *pachachacae*, *piperata*, and *splendens*.

Gastrotheca antoniiochoai differs from *G. zeugocystis* by having a tibia that is slightly more than 50% of the snout–vent length, compared with 46% in *G. zeugocystis*; the tibia is longer than the foot in *G. antoniiochoai*, whereas the segments are equal in length in *G. zeugocystis*. The first finger is shorter than the second in *G. antoniiochoai*, but the two fingers are equal in length in *G. zeugocystis*. The two species differ in markings on the head: a dark brown canthal-postorbital stripe is present in *G. antoniiochoai*, whereas the stripe is absent in *G. zeugocystis*. The largest brooding female *G. antoniiochoai* has a snout–vent length of 32.5 mm, and the largest *G. zeugocystis* female has a snout–vent length of 37.5 mm.

Description

The following description is based on eight specimens. The body is slightly depressed. The maximum known snout–vent length is 26.8 mm in males, and 32.5 mm in females. The head is about as wide as long, and slightly narrower than the body. The snout is broadly rounded in dorsal view, and is truncate in profile. The canthus is slightly curved, and is rounded in cross-section. The loreal region is shallowly concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 85% of the width of the upper eyelid. The nostrils are not protuberant, and are directed laterally just below the anterior terminus of the canthus rostralis at the level of the anterior margin of the lower jaw. The diameter of the eye is much greater than its distance from the nostril. The tympanum is distinct, round, and separated from the eye by a distance about equal to the diameter of the eye. The tympanic annulus is smooth. The supratympanic fold is rounded; it covers the upper edge of the tympanum, and then curves posteroventrally to a point above the insertion of the arm.

The arm is moderately slender, and lacks ulnar tubercles. The hand is proportionately large. The fingers are moderately long, and bear round discs; the width of the disc on the third finger is barely wider than the digit proximal to the disc. The relative lengths of the fingers are I < II < IV < III. The fingers are unwebbed, and lack lateral fringes. The subarticular tubercles are moderately large and round; the distal subarticular tubercles on some fingers are weakly bifid. The supernumerary tubercles are slightly elevated, and are round on the proximal segments of the fingers. The palmar tubercle is weakly developed, and is only about half the size of the prominent round prepollical tubercle; brown nuptial excrescences are present on the thumbs of adult males. The hind limb is moderately slender. The tibia length is about 51% of the snout–vent length; the foot length is about 47% of the snout–vent length. The heels lack a calcar or tubercle. Tarsal tubercles and inner and outer tarsal folds are absent. The inner metatarsal tubercle is oval, and is not visible from above. The toes are moderately long, and bear round discs the same size as those on the fingers. The relative lengths of the toes are I < II < III < V < IV. The toes are unwebbed, except for basal webbing between the third and fourth and the fourth and fifth toes. The toes lack lateral fringes. The subarticular tubercles are low and round; the distal tubercles of Toes III–V are weakly bifid; the supernumerary tubercles are round, and are most evident in the proximal segments of the digits.

The skin on the dorsum is weakly shagreen, not co-ossified with the underlying cranial elements, and lacks transverse dermal ridges. The skin on the flanks also is shagreen; the skin on the throat, chest, belly, and posteroventral surfaces of the thighs is coarsely granular; the other ventral surfaces are smooth. Supraciliary processes are absent. The supratympanic fold is tubercular; there are no tubercles below the cloacal opening. The brood pouches are paired; the external margin of the brood pouch is elongately narrow and U-shaped; the opening to each pouch is under the lateral dermal fold, and extends broadly ventrolaterally to a pouch between the body wall and the skin. The dentigerous processes of the vomers are low, and are positioned obliquely between the small oval choanae.

COLOR IN PRESERVATIVE

The dorsal surfaces of the head and body are gray, with small dark brown flecks; the dorsal surfaces of the limbs are beige, with or without dark brown transverse bars. The flanks and belly are gray, with minute black flecks evident on the belly. The ventral surfaces of the limbs are cream; the throat is paler cream. A dark gray canthal-postorbital stripe is evident; there are no other markings on the head.

COLOR IN LIFE

The dorsum varies from golden tan to reddish brown, with or without dark brown and/or green flecks (Fig. 12.5). In some individuals the limbs are tan with brown flecks, whereas in others they are brown with cream flecks, or pale brown with dark brown transverse bars. The side of the head is darker than the dorsum; the canthal-postorbital stripe is dark brown; other markings are absent on the head. In adults all ventral surfaces are homogeneously grayish brown or beige, with numerous minute black melanophores; in juveniles the throat, chest, and belly are white. The iris is reddish bronze in adults, and bronze with black reticulations in juveniles.

MEASUREMENTS

The measurements (in mm) of two adult males are followed by those of one adult female (Catenazzi and

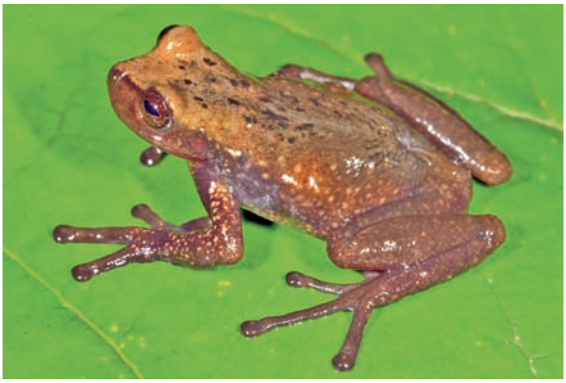

Fig. 12.5 *Gastrotheca antoniiochoai* (MUSM 27949), female, 32.5 mm SVL, Wayquecha Research Station, 2950 m, Cusco, Peru. Photo by A. Catenazzi, KUDA.

Lehr, 2009): snout–vent length 26.8, 27.0, 32.5; tibia length 13.2, 14.0, 16.5; foot length 12.4, 13.0, 17.1; head length 8.9, 9.0, 10.3; head width 8.8, 9.1, 11.8; interorbital distance 2.9, 3.2, 3.5; eyelid width 2.0, 2.4, 2.7; internarial distance 1.4, 1.5, 1.8; eye diameter 2.9, 3.0, 3.4; eye–nostril distance 2.3, 2.5, 2.7; orbit–jaw distance 1.4, 1.5, 1.7; nostril–jaw distance 1.8, 2.1, 2.4; tympanum length 1.3, 1.6, 1.6; thumb length 3.0, 4.2, 5.8; third finger length 8.0, 8.3, 10.1; and width of disc on third finger 1.1, 1.3, 1.6.

Another male has a snout–vent length of 28.6 mm, and two juveniles have snout–vent lengths of 13.4 and 14.1 mm.

CRANIAL OSTEOLOGY

No data are available.

Life History

The single known adult female contained six eggs, each about 6.5 mm in diameter (Catenazzi and Lehr, 2009); a photograph of this female shows three eggs in each lateral pouch. The small number and large size of the eggs are indicative of completion of development within the pouches; presumably this species has direct development of eggs into froglets.

Advertisement Call

Catenazzi and Lehr (2009) obtained recordings of 15 calls of one male (MUSM 27948) at 20°C. They described the advertisement call as a long note, 412–601 milliseconds ($\bar{x} = 544.8 \pm 27.5$) in duration, with 26–38 pulses ($\bar{x} = 33.6 \pm 1.9$) and one, two, or three single-pulsed short secondary notes, 17–22 milliseconds ($\bar{x} = 21.3 \pm 1.8$) in duration. The call frequency was 18–40 calls per minute ($\bar{x} = 32.2 \pm 6.4$), and the call length was 377–674 milliseconds ($\bar{x} = 603.3 \pm 70.3$). The long notes displayed little frequency modulation, and the range of fundamental frequency was 2544–2968 Hz (median = 2915 Hz). The dominant frequency in short notes was 1749–3445 Hz, with maximum call energy at 3180–3445 Hz (median = 3286 Hz). The interval between long and short notes was 192–277 milliseconds ($\bar{x} = 218.0 \pm 22.8$).

Distribution and Ecology

This species is known only from montane scrub and cloud forest at elevations of 2800–3300 m in the upper Kosñipata Valley on the Amazonian versant of the Cordillera Oriental in southern Peru (Fig. 12.6). The holotype was in a fallen arboreal bromeliad. Subsequent specimens were found 6–8 m above the ground, in bromeliads (Catenazzi and Lehr, 2009).

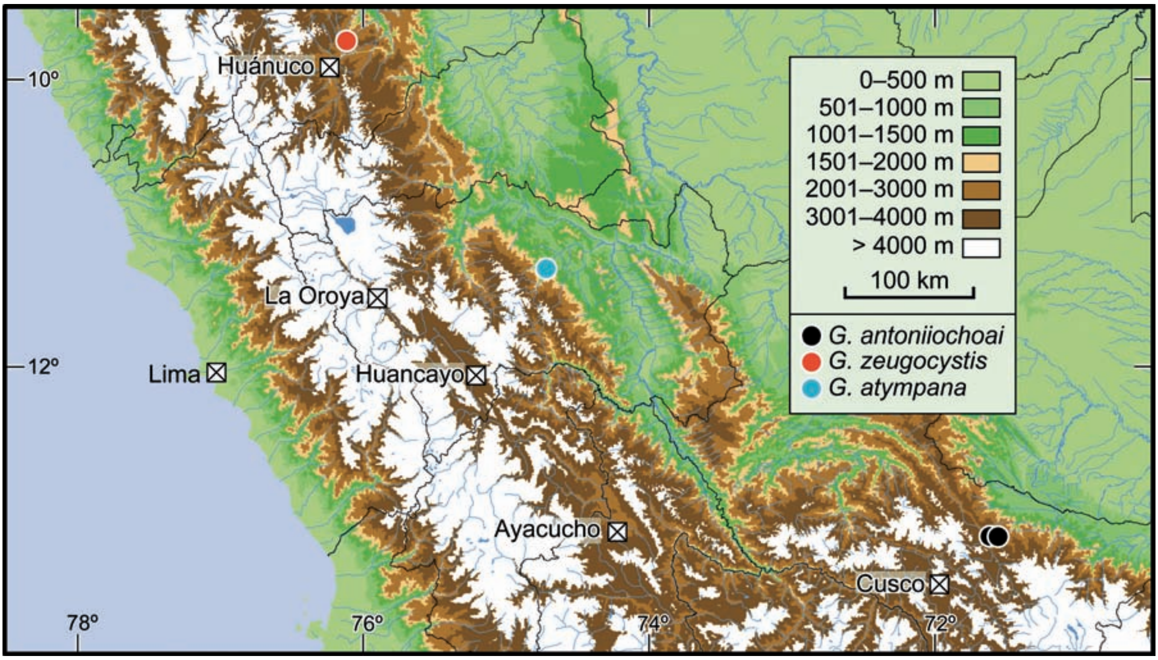

Fig. 12.6 Andean region of Peru, showing the localities of known occurrences of *Gastrotheca antoniiochoai*, *atympana*, and *zeugocystis*.

Conservation Status

In the IUCN Red List, *Gastrotheca antoniiochoai* is listed as Data Deficient; it was noted as occurring in the Manu Biosphere Reserve.

Etymology

According to De la Riva and Chaparro (2005), the specific name *antoniiochoai* is a patronym for the Peruvian biologist Antonio Ochoa.

Remarks

The original description was based on a subadult female and a juvenile (De la Riva and Chaparro 2005). The authors noted that the female contained immature white ovarian eggs, fat bodies, and undeveloped oviducts. Although undeveloped (non-convoluted) oviducts are characteristic of immature females, De la Riva and Chaparro erroneously considered the specimen to be a mature female. Consequently, they placed the species in the genus *Hyla*, according to how this genus was recognized prior to the study by Faivovich et al. (2005). Catenazzi and Lehr (2009) reported on an adult female that was brooding eggs, and they placed the species in *Gastrotheca*. Lateral brooding pouches are known only in *G. antoniiochoai* and *G. zeugocystis*, a species that apparently is a distant relative of *G. antoniiochoai*. *G. walkeri* and *G. williamsoni* also have lateral brood pouches, but in those two species the pouches are retroperitoneal, inasmuch as they penetrate the body wall; thus the young develop within the coelomic cavity.

Catenazzi and Lehr (2009) noted that *G. antoniiochoai* seems to be highly adapted for life in bromeliads. The frogs can flatten their bodies considerably in order to fit between the leaves of the bromeliads, and they can quickly "walk" backward, a movement that is useful when retreating into bromeliads. These authors suggested that the presence of lateral pouches is an adaptation for life in bromeliads, because with lateral pouches the female's body remains flat and thin by having eggs on the flanks, rather than on the dorsum. Having a flat thin body facilitates hiding at the base of bromeliads, where the space between the leaves is narrow.

Gastrotheca (*Gastrotheca*) *aratia* Duellman, Barley, and Venegas

Gastrotheca aratia Duellman, Barley, and Venegas, 2014: 170.—Holotype: KU 212067 from 8 km [by road] NW Cutervo, 2560 m, Región de Cajamarca, Peru.

Diagnosis

Adults of this moderately large species attain snout–vent lengths of 57 mm. The tibia length is slightly less than 50% of the snout–vent length, about the same length as the foot. The interorbital distance is slightly less than the width of the upper eyelid. The skin on the dorsum is granular, not co-ossified with skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. Finger I is shorter than II. The discs on the fingers are slightly wider than the digits. The fingers are unwebbed; on the foot the webbing extends maximally to the penultimate subarticular tubercle on Toe IV and nearly to the penultimate subarticular tubercle on Toe V. The dorsum is green or brown, with darker paravertebral marks and an inverted V-shaped mark posterior to the sacrum. Markings on the head consist of a dark canthal stripe and a pale labial stripe. A pale dorsolateral stripe usually is present. The flanks and the anterior and posterior surfaces of the thighs lack dark markings; the venter is cream, with faint dark flecks or spots.

Gastrotheca aratia most closely resembles four other species in northern Peru. In contrast to the much larger *G. monticola*, *G. aratia* usually lacks a pale supracloacal stripe and black spots on the flanks and anterior and posterior surfaces of the thighs. The slightly smaller *G. aguaruna* differs by having dark marks in the groin, webbing extending only to the antepenultimate subarticular tubercle on Toe IV, and a tarsal fold only on the distal half of the tarsus. *G. dysprosita* differs from *G. aratia* by having a green dorsum with a narrow yellow middorsal stripe, and green flanks with small yellow spots; furthermore, *G. dysprosita* lacks a dark canthal stripe and pale labial stripe. *G. lateonota* is like *G. monticola* in size and in most proportions, but *G. lateonota* differs from *G. aratia* and *G. monticola* by having a truncate snout in profile, smooth skin on the dorsum, and a nearly uniform grayish-brown venter. Five other species of *Gastrotheca* are present in the Andes in northern Peru. *G. peruana*, *G. phalarosa*, and *G. phelloderma* all have pustular skin on the dorsum. *G. abdita* has an acuminate snout in dorsal view. *G. galeata* differs from all of the the others by having a spatulate labium. The latter two species also produce eggs that undergo direct development, whereas *G. aratia* produces eggs that hatch as tadpoles.

Description

The following description is based on nine specimens. The body is robust; the only brooding female (snout–

vent length 56.8 mm) is slightly larger than the largest male (snout–vent length 55.7 mm). The head is slightly wider than long. The snout is rounded in dorsal view, and is bluntly rounded in profile, extending slightly beyond the margin of the lower lip. The canthus rostralis is acutely rounded in cross-section. The loreal region is barely concave; the lips are rounded. The top of the head is flat. The interorbital distance is slightly less than the width of the upper eyelid. The internarial area is flat. The nostrils are not protuberant, and are located at the terminus of canthus rostralis posterior to the level of the anterior margin of the lower jaw. The diameter of the eye is slightly greater than its distance from the nostril. The tympanum is round, and is separated from the eye by a distance about equal to the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is weak, and extends from the posterior corner of the orbit to a point posterior to the tympanum. The arm is robust; ulnar tubercles are absent. The hand is moderately large. The fingers are short and unwebbed. The discs in the fingers are moderately large and rounded; the width of the disc on Finger III is equal to half the length of the tympanum. The relative lengths of the fingers are I > II < IV < III. The subarticular tubercles are prominent, low, and rounded; none are bifid. Supernumerary tubercles are not evident. The palmar tubercle is absent; the prepollical tubercle is elliptical; calling males have no evident nuptial excrescences. The hind limbs are robust. The mean tibia length is 44.7% of the snout–vent length; the mean foot length is 44.2% of the snout–vent length. A calcar and tarsal tubercles are absent. The inner tarsal fold extends the entire length of the tarsus. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is large, elliptical, and not visible from above. The toes are long. The relative lengths of the toes are I < II < III < V < IV. The webbing is basal between Toes I and II; the webbing formula for the other toes is **II**2—2**III**2—3**IV**3—1**V**. The subarticular tubercles are small and rounded; supernumerary tubercles are absent. The skin on the dorsum and flanks is smooth; the skin on the throat, belly, and ventral surfaces of the thighs is granular; the other surfaces are smooth. Cloacal tubercles and folds are absent. The pouch opening is puckered. The dentigerous processes of the vomers are inclined posteromedially, and are narrowly separated medially between the round choanae. Each process bears four or five teeth.

COLOR IN PRESERVATIVE

The dorsum is brown to pale gray, with darker gray or brown markings consisting of broad paravertebral marks extending from the eyelids to the sacrum and to a narrower V-shaped postsacral mark with the apex positioned anteriorly. The dorsal surfaces of the limbs vary from having no definite markings to having transverse bars nearly was wide as the interspaces: as many as two on the forearm, four on the thigh, three on the shank, and two on the tarsus. A white labial stripe, dark brown canthal stripe, and broad postorbital bar are present; in some specimens the postorbital bar extends to the middle of the flank. Three individuals have a narrow cream dorsolateral stripe extending from the margin of the upper eyelid to the groin; two specimens have a discontinuous supracloacal white stripe. The venter is creamy tan, with or without small dark brown flecks on the chest. The vocal sac in calling males is brown.

COLOR IN LIFE

The dorsum is green or tan, with faint to distinct darker green or brown paravertebral marks originating on the upper eyelids and becoming indistinct on the anterior part of the body (Fig. 12.7). A narrow brown canthal stripe and a distinct white labial stripe are present. The postorbital region and the flanks are mottled green and tan. The iris is silvery bronze, with fine black flecks and reticulations.

MEASUREMENTS

Males are slightly smaller than females (Table 12.2).

CRANIAL OSTEOLOGY

No skeletal preparations exist.

Life History

Brooding females contain large numbers of eggs that hatch as tadpoles.

Tadpoles

Metamorphosing young and tadpoles in two stages of development were found in a cistern at Cutervo, Región de Cajamarca, Peru, on 26 February 1989. A tadpole in Stage 36 (KU 212498) has a body length of 21.2 mm, and a total length of 56.4 mm. In dorsal view the body is elongately ovoid, and widest at midlength of the body; the snout is bluntly rounded. In profile the body is highest at about two-thirds the length of the body, wider than high, and gradually inclined to a rounded snout. The throat is convex. The eyes are small, and are directed dorsolaterally. The interorbital distance is about one-third the width of the body at the level of the orbits. The nostrils are about midway between the eyes and the tip of the snout. The spiracu-

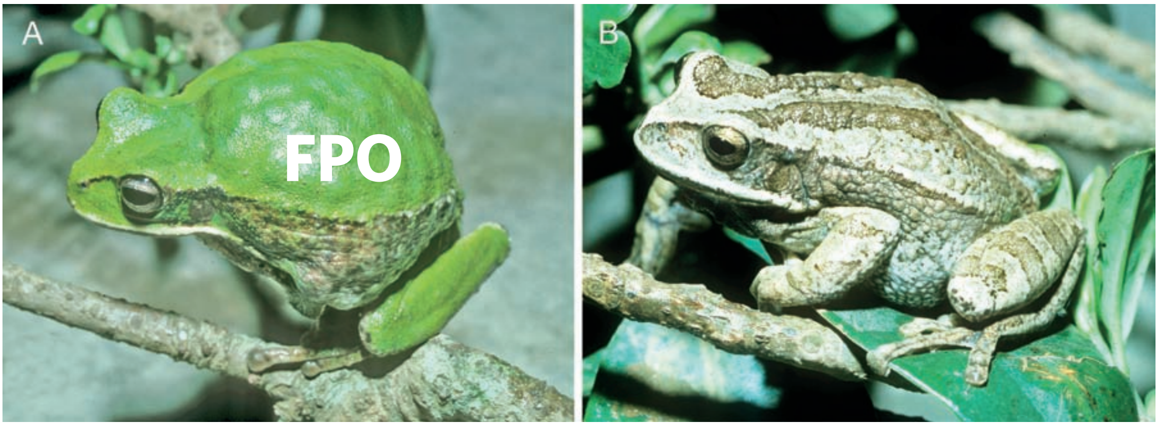

Fig. 12.7 *Gastrotheca aratia*. A: KU 212067 (holotype), female, 54.7 mm SVL, 8 km NW Cutervo, Cajamarca, Peru. B: KU 212055, male, 51,5 mm SVL, vicinity of Cutervo, Cajamarca, Peru. Photos by M. E. Morrison, KUDA.

lar tube is short, and is attached to the body throughout its length. The spiracular opening is directed posterolaterally on the ventrolateral surface of the body at a point about 62% of the length of the body. The cloacal tube is short, conical, dextral, and attached to the ventral fin for its entire length; the cloacal opening is transverse. The caudal musculature is moderately robust, and is much higher than the dorsal fin at midlength of the tail. The musculature terminates in a pointed tip just short of the margin of the caudal fin. The dorsal fin arises gradually from the proximal part of the caudal musculature. The height of the dorsal fin is about equal to that of the ventral fin at midlength of the tail; the fins terminate in an acutely rounded tip.

The width of the oral disc is about one-third the width of the body. The disc is bordered laterally by a single row of short blunt marginal papillae, and ventrally by two rows of alternating papillae. There are two upper and three lower rows of labial teeth; the upper rows are slightly longer than the lower ones, and are subequal in length; the lower rows are progressively shorter; the second upper row is interrupted medially. The upper jaw sheath is moderately heavy, and is broadly arch-shaped; the lower sheath is slightly more robust, and is broadly V-shaped. Both sheaths bear low blunt serrations.

In preservative the body is dull brown. The skin on the ventrolateral surfaces and the venter is unpigmented. The caudal musculature is cream, with a brown streak along the upper edge. The fins are translucent, with fine brown reticulations. The coloration in life is not known.

Tadpoles in Stages 25–30 were found with the larger tadpole. The smallest individual in Stage 29 has a body length of 9.4 mm, and a total length of 26.3 mm; the mouthparts are complete; the brown streak is evident on the dorsal caudal musculature. Two metamorphosing young have snout–vent lengths of 23.3 and 25.7 mm, and tail stubs 9.6 and 9.8 mm long, respectively.

Advertisement Call

The call consists of a low guttural note, usually followed by two or three shorter notes. No recordings are available.

Distribution and Ecology

Gastrotheca aratia is known from elevations of 2560–2875 m in the northern part of the Cordillera Occidental of the Andes in northwestern Peru (Fig. 12.3). The holotype was turned up in a plowed field by day; most of the terrain in the immediate vicinity of Cutervo is cultivated. Three males were calling from low bushes on a rainy night. All adults were found in or at the edge of plowed fields. Tadpoles and two young individuals were found in a cistern. All other specimens were extracted from terrestrial spiny bromeliads by day.

Conservation Status

Gastrotheca aratia is only known to occur in cultivated areas, and thus seems to be surviving under unnatural conditions. Possible use of herbicides or chemical fertilizers would endanger the species. Thus *G. aratia* should be categorized as Vulnerable in the IUCN Red List.

Etymology

According to Duellman et al. (2014), the specific name is derived from the Latin noun *aratio*, meaning "plowed field."

Remarks

In the tree of proposed phylogenetic relationships provided by Duellman et al. (2014), *Gastrotheca aratia* is the sister species to *G. peruana*, a species that is widespread in the Andes of northern and central Peru.

Gastrotheca (*Gastrotheca*) *atympana* Duellman, Lehr, Rodríguez, and von May

Gastrotheca atympana Duellman, Lehr, Rodríguez, and von May, 2004:2.—Holotype: MUSM 18692 from Pampa Hermosa (10°59′33.3″ S, 75°25′58.0″ W), 1540 m, Provincia de Tarma, Región de Junín, Peru.

Diagnosis

In this medium-sized species (males to 46.7 mm), the tibia length is 51.6% of the snout–vent length, much longer than the foot. The interorbital distance is more than twice the width of the upper eyelid. The skin on the dorsum is shagreen, not co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel has a transverse row of small tubercles. A tympanic annulus is absent. The first finger is shorter than the second. The discs are much wider than the digits. The fingers are unwebbed; on the foot the webbing extends to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is tan, with irregular transverse brown markings. Markings on the head consist of a broad dark brown interocular bar and pale labial and canthal-postorbital stripes. A pale dorsolateral stripe is absent. The flanks are cream, with irregular vertical black marks; the venter is pale tan.

Gastrotheca atympana differs from all other members of the genus by lacking an external tympanum. Seven other species of *Gastrotheca* have a tibia length that is 50%–55% of the snout–vent length, and the first finger shorter than the second. Of these, *G. antomia* differs by having supraciliary processes, two tubercles on the heel, and a venter that is orange or red anteriorly and black posteriorly. *G. orophylax* differs by being uniformly green dorsally and ventrally, except for a cream labial stripe. *G. argenteovirens* and *G. dunni* differ by having pale dorsolateral stripes. *G. psychrophila* differs by having a uniformly brown to dull green or nearly black dorsum, and basal webbing between the fingers. *G. ochoai* and *G. rebeccae* differ by having a narrower interorbital region (interorbital distance about 1.5 times the width of upper eyelid); the former is smaller (snout–vent length to 38 mm) and lacks an interocular bar, whereas the latter is about the same size as *G. tympana*, but the markings on the head consist of a dark canthal stripe in addition to a dark interocular bar and pale labial stripe. Two other larger species have vertical black bars on the flanks. Of these, *G. ovifera* has the skin co-ossified with the skull, and has a prominent transverse occipital ridge; *G. testudinea* has the first finger longer than the second, and is like *G. ovifera* in having the webbing extending to the distal subarticular tubercle on the fifth toe, as opposed extending only to the penultimate tubercle in *G. atympana*.

Description

The following description is based on the holotype (the only known specimen), an adult male. The body is moderately slender; the snout–vent length is 46.7 mm. The head is wider than long, and about as wide as the body. The snout is narrowly truncate in dorsal view, rounded above, and slightly inclined anteroventrally in profile. The canthus rostralis is curved, and is angular in cross-section. The loreal region is barely concave; the lips are not flared. The top of the head is flat. The interorbital distance is 240% of the width of the upper eyelid. The internarial area is barely concave. The nostrils are slightly protuberant, and are directed laterally just below the anterior terminus of the canthus rostralis at a level posterior to the anterior margin of the lower jaw. The diameter of the eye is slightly greater than its distance from the nostril. The tympanum is not differentiated. A tympanic annulus is absent. The supratympanic fold is elevated, angular, deflected laterally, and continuous with a distinct nearly vertical fold extending ventrally to a point just above the insertion of the arm.

The arm is moderately robust; a row of small ulnar tubercles is barely evident. The hand is large. The fingers are long, and bear large round discs; the width of the disc on the third finger is nearly twice the width of the penultimate segment of the finger. The relative lengths of the fingers are I < II < IV < III. The fingers are unwebbed, and bear narrow lateral fringes on Fingers II–IV. The subarticular tubercles are moderately large and round; none are bifid. The supernumerary tubercles are subconical, and are nearly as large as the subarticular tubercles. The palmar tubercle is diffuse; the prepollical tubercle is elongate and elliptical; nuptial excrescences are not evident. The hind limb is slender. The tibia length is 51.6% of the snout–vent length; the foot length is 40.7% of the snout–vent length. The heels bear transverse rows of five or six small tubercles. Tarsal tubercles are absent; the inner tarsal fold is low and weak on the distal three-fourths of the tarsus; a low crenulated outer tarsal fold extends from the heel to the disc on the fifth toe. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is small, elliptical, and visible from above. The toes are long, have narrow lateral fringes distally, and bear round terminal discs about the same size as those on the fingers. The relative lengths of the toes are I < II < III = V < IV. The toes are less than one-half webbed; the webbing formula is **I**2–2½**II**2–3^{+}**III**2–3**IV**2^{-}–1^{-}**V**. The subarticular tubercles are large and round; the supernumerary tubercles are small and diffuse.

The skin on the dorsum is finely shagreen, with many small subconical tubercles in the temporal region; the skin on the head is not co-ossified with the underlying cranial elements; the skin on the flanks is areolate; the skin on the throat, chest, belly, and posteroventral surfaces of the thighs is coarsely granular; the other ventral surfaces are smooth. Transverse dermal ridges and supraciliary processes are absent. There is a transverse row of five subconical tubercles below the cloacal opening. The shape of the opening of the brood pouch is unknown. Vocal slits are absent; the vocal sac is not evident. The dentigerous processes of the vomers are elevated, posteromedially inclined, and narrowly separated medially between the posterior margins of the ovoid choanae. Each process bears six teeth.

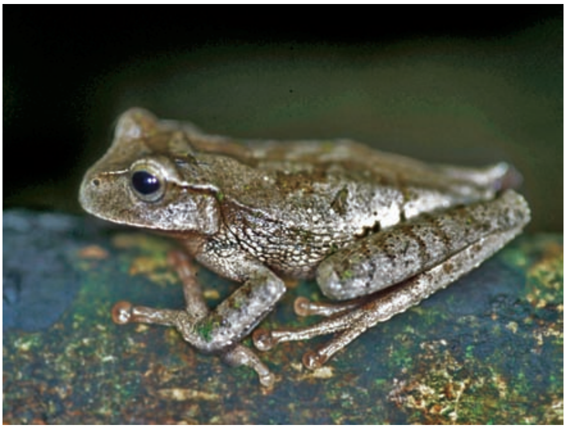

Fig. 12.8 *Gastrotheca atympana* (MUSM 18692, holotype), male, 46.7 mm SVL, Pampa Hermosa, 1540 m, Junín, Peru. Photo with permission granted by the photographer, E. Lehr. Copyright 2003. All rights reserved.

COLOR IN PRESERVATIVE

The dorsum of the head and body are grayish tan, with dull brown markings consisting of a broad interorbital bar connected to a triangular mark in the scapular region and irregular marks posteriorly on the body. The dorsal surfaces of the limbs are pale gray, with narrow transverse bars: three on each forearm, thigh, and foot, and six or seven on the shanks; the bars on the thighs are continuous onto the anterior surfaces. The flanks are pale brown anteriorly and pale grayish white posteriorly, with four or five irregular vertical black marks; the interstices in the areolate skin on the flanks are black. The side of the head is pale grayish tan. A narrow creamy white stripe extends from a point just behind the nostril, along the canthal crest, to the edge of the upper eyelid, and then to the edge of the supratympanic fold; it is bordered below by a narrower brown stripe in the loreal and temporal regions. The margin of the upper lip is creamy white. The posterior surfaces of the thighs are dark brown, with dorsal triangular extensions contiguous with the transverse bars on the dorsal surfaces. The tubercles on the ventrolateral edges of the forearms, on the heel, below the cloacal opening, and on the fold on the outer edge of the foot are white. The throat is cream; the chest, belly, and palmar surfaces are pale brown; the ventral surfaces of the limbs and plantar surfaces are pale grayish brown.

COLOR IN LIFE

The dorsum and flanks are pale grayish tan. The dorsal markings are orange brown, with narrow dark brown edges; the labial and canthal-postorbital stripes are pale beige, narrowly bordered below by brown (Fig. 12.8). The fringe on the foot and the ulnar and subcloacal tubercles are white; the dorsal surfaces of the discs and the distal parts of the digits are orange brown. The posterior flanks are pale gray to white, with black markings. The throat is pale beige, with chocolate brown blotches; the belly is chocolate brown. The palmar and plantar surfaces are dark gray. The iris is pale yellowish tan above and pale gray below, with fine black reticulations.

MEASUREMENTS

The measurements (in mm) of the single male specimen are as follows: snout–vent length 46.7, tibia length 24.1, foot length 19.0, head length 15.1, head width 17.2, interorbital distance 7.2, upper eyelid width 3.0, internarial distance 2.6, eye diameter 4.5, eye–nostril distance 3.9, orbit–jaw distance 2.4, nostril–jaw distance 2.6, thumb length 6.5, third finger length 13.5, and width of disc on third finger 1.9.

CRANIAL OSTEOLOGY

No data are available.

Life History

No data are available; presumably the eggs of this species hatch as froglets.

Distribution and Ecology

The species is known only from the type locality, at an elevation of 1540 m in the valley of the Río Chanchamayo, a broad intrusion into the Cordillera Oriental in central Peru (Fig. 12.6). The holotype was 1.2 m above the ground on a branch of a tree at 2100 hours.

Conservation Status

This poorly known species is categorized as Data Deficient in the IUCN Red List. Duellman et al. (2004) noted that the type locality is a locally protected dense and humid montane forest.

Etymology

According to the original description (Duellman et al., 2004), the specific name is derived from the Greek prefix *a*-, meaning "without," and the Greek *tympanion*, meaning "eardrum"; the name is used as an adjective noting the absence of a tympanum.

Remarks

A juvenile (CORBIDI 11040) from Quintecocha, Región de San Martín, Peru, has a barely discernable tympanum, but this specimen probably is not conspecific with *Gastrotheca atympana*.

Gastrotheca (*Gastrotheca*) *caeruleomaculata* (Werner)

Hylodes caeruleomaculatus Werner, 1899:482.—Syntypes: NMW 16496 (2 specimens) from "Bolivia."

Nototrema bolivianum (in part)—Nieden, 1923:320.

Gastrotheca lauzuricae De la Riva, 1992:18.—Holotype: CET A501 from La Siberia, 2800 m, Provincia de Carrasco, Departamento de Cochabamba, Bolivia. New synonymy.

Diagnosis

In this moderately small species of *Gastrotheca* (females to 45.1 mm), the tibia length is about 48% of the snout–vent length, and is about as long as the foot. The interorbital distance is slightly more than the width of the upper eyelid. The skin on the dorsum is smooth, not co-ossified with skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is shorter than the second. The discs on the fingers are much wider than the digits. The fingers are unwebbed; on the foot the webbing extends maximally to the preantepenultimate subarticular tubercle on the fourth toe and the antepenultimate subarticular tubercle on the fifth toe. The dorsum is tan with brown, green, and blue blotches or flecks. Markings on the head consist of a narrow dark brown canthal stripe and a wider brown postorbital stripe. A pale dorsolateral stripe is absent. The flanks are tan, with brown and blue blotches; the venter is cream.

The sympatric *Gastrotheca piperata* differs by having a dorsal color pattern consisting of black flecks instead of the blue blotches in *G. caeruleomaculata*, a dorsal pattern unknown in any other species of the genus. The geographically proximal *G. marsupiata* lacks blue blotches on the dorsum, and usually has a dark brown interorbital bar and longitudinal dark marks on the dorsum.

Description

The following description is based on 11 specimens. The head is slightly wider than long. The snout is rounded in dorsal view and in profile. The canthus rostralis is straight, and is acutely rounded in cross-section. The loreal region is shallowly concave; the lips are rounded. The top of the head is flat. The interorbital distance is slightly greater than the width of the eyelid. The internarial area is barely depressed. The nostrils are slightly protuberant, and are directed laterally at a point slightly posterior to the anterior margin of the lower jaw. The diameter of the eye is much greater than its distance from the nostril. The tympanum is nearly round, and is separated from the eye by a distance about twice the length of the tympanum. The tympanic annulus is distinct and smooth. The weak supratympanic fold extends from the posterior corner of the orbit to a point above the insertion of the arm; the fold barely obscures the upper edge of the tympanum.

The arm is moderately robust; ulnar tubercles are absent. The hand is moderately small. The fingers are moderate in length, and are unwebbed. The discs are moderately large and round; the width of the disc on the third finger is about equal to the length of the tympanum. The relative lengths of the fingers are I < II < IV < III. The subarticular tubercles are large, and are round to subconical; the supernumerary tubercles are large, round to subconical, and numerous on the proximal segments of the digits. The palmar tubercle is small and subconical; the prepollical tubercle is moderately large and elliptical; in males a brown nuptial excrescence is present on the median surface of the thumb. The hind limb is moderately robust. The tibia length is 48.7% of the snout–vent length; the foot is slightly shorter than the tibia. The heel lacks a calcar or tubercle. Tarsal tubercles and an inner tarsal fold are absent. The inner metatarsal tubercle is elliptical, elevated, and not visible from above; the outer metatarsal tubercle is diffuse or absent. The toes are moderately long, and bear discs about the same size as those on the fingers. The relative lengths of the toes are I < II < III = V < IV. Webbing is absent between Toes I and II; the outer toes are webbed basally. The subarticular tubercles are moderately small and rounded; the supernumerary tubercles are small, low, and few in number on the proximal segments of the digits.

The skin on the dorsum and flanks is smooth; the skin on the belly and posteroventral surfaces of the thighs is coarsely granular. Cloacal tubercles and folds are absent. The opening of the brood pouch is U-shaped, with the anterior margin at the level of the posterior edge of the sacrum. The dentigerous processes of the vomers are transverse, narrowly separated medially, and between the small choanae. Each process bears four or five teeth.

COLOR IN PRESERVATIVE

The dorsal surfaces of the head, body, and limbs are gray to brown, with small irregular darker brown marks on the head and body, and transverse marks on the limbs: one on the upper arms, and two each on the forearms, thighs, shanks, and feet. Transverse bars on the limbs are absent in CGB 1018. In four specimens (CGB 1017, 1020, 1034–35), irregular pale gray blotches are present on the dorsal surfaces of the head and body. Markings on the head consist of a narrow dark brown canthal stripe and a broad dark brown postorbital stripe. An interorbital bar is absent. The canthal region and lips are gray or tan, with or without small brown marks on the latter. The flanks are brown, with cream spots or mottling. The posterior surfaces of the thighs are either grayish tan with cream mottling, tan with brown mottling, or uniformly tan. The anterior surfaces of the thighs and all ventral surfaces are creamy tan, with or without small indistinct gray flecks on the chin, chest, and belly. The vocal sac is brown.

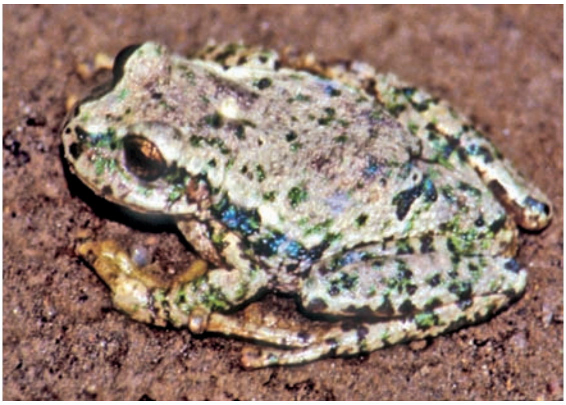

Fig. 12.9 *Gastrotheca caeruleomaculata* (CET A501, holotype of *G. lauzuricae*), female, 35.8 mm SVL, La Siberia, 2550 m, Cochabamba, Bolivia. Photo by I. De la Riva, KUDA.

COLOR IN LIFE

Information on coloration in life is taken from De la Riva (1992) and the photograph of the holotype of *Gastrotheca lauzuricae*. The dorsum of the head and body is pale tan, becoming creamy tan dorsolaterally and on the anterior snout. Small dark brown, emerald-green, and bright blue spots or flecks are present on the head and body (Fig. 12.9). Transverse bars on the limbs are irregularly dark brown or green; the interspaces are tan. The posterior surfaces of the thighs are orange tan; the venter is cream. The iris is bronze, with fine black reticulations.

MEASUREMENTS

Females are somewhat larger than males (Table 12.3).

CRANIAL OSTEOLOGY

No data are available.

Life History

One female (CGB 1019) with a snout–vent length of 41.6 mm contains at least 10 ovarian eggs, each

Table 12.3 Measurements for adults of *Gastrotheca caeruleomaculata*

	Males (*n* = 4)		Females (*n* = 7)	
Character	Mean	Range	Mean	Range
Snout–vent length	33.7	28.8–36.1	41.6	35.8–45.2
Tibia length	15.9	14.2–17.2	19.9	17.9–21.2
Foot length	15.6	12.9–16.9	20.2	16.6–21.9
Head length	11.4	9.9–12.6	13.2	12.3–14.0
Head width	11.9	11.0–12.5	14.2	13.2–14.9
Interorbital distance	3.7	3.2–4.1	4.4	3.8–4.7
Eyelid width	3.2	3.0–3.5	3.5	3.0–3.8
Internarial distance	2.7	2.5–2.9	3.1	2.9–3.5
Eye diameter	4.3	3.8–4.4	4.1	3.5–4.8
Eye–nostril distance	3.8	2.9–4.5	4.1	3.4–4.9
Orbit–jaw distance	2.3	2.2–2.4	2.3	2.0–2.8
Nostril–jaw distance	2.9	2.8–3.0	3.0	2.7–3.4
Tympanum diameter	2.5	1.9–2.8	2.8	2.2–3.2
Thumb length	5.6	4.8–6.5	6.8	4.5–7.7
Third finger length	12.8	10.2–16.3	13.6	11.1–14.7
Disc width	2.1	1.9–2.3	2.0	1.9–2.1

± 3.2 mm in diameter. Another female having a snout–vent length of 41.6 mm contains 20 eggs, each about 5 mm in diameter, in the brood pouch. The number and size of these ovarian eggs is comparable to those of *Gastrotheca ochoai*, which produces eggs that hatch as froglets. Examination of developing young in the brood pouches of two other females indicates that the eggs of *G. caeruleomaculata* undergo direct development.

Distribution and Ecology

This species is known definitely from three localities, at elevations of 2000 and 2800 m on the eastern flank of the Cordillera Oriental of the Andes in central Bolivia (Fig. 12.10). The species inhabits cloud forest. The holotype was under a rock by day.

Conservation Status

This species has not been categorized in the IUCN Red List.

Etymology

The specific name is derived from the Latin *caeruleus*, meaning "sky blue," and the Latin *maculatus*, meaning "spotted." The name refers to the blue spots on the dorsum and flanks.

Remarks

As has happened several times, small males of Andean *Gastrotheca* have been described as new species of *Hylodes* or *Eleutherodactylus*. Neither syntype of *H. caeruleomaculatus* is a female with a dorsal pouch; the largest specimen is a male with a snout–vent length of 28.8 mm. Without any justification, Nieden (1923: 320) listed *H. caeruleomaculatus* Werner, 1899, as a junior synonym of *Nototrema bolivianum* Steindachner, 1892; the latter was placed in the synonymy of *G. marsupiata* Duméril and Bibron, 1841, by Duellman and Fritts (1972:4).

Werner's (1899) description of *Hylodes caeruleomaculatus* was based on two specimens (NMW 16496) from "Bolivien." The largest individual is a male having a snout–vent length of 28.8 mm. Werner (1899:483) described the coloration as follows: "Dorsum bright gray with large bright blue black-bordered flecks; or with bright grayish blue, less dark border (other example). On the dorsum of the limbs transverse bands instead of flecks. A young example almost plain grayish blue. Underside yellowish white" [literal translation from German].

De la Riva (1992) described *Gastrotheca lauzuricae* from La Siberia, Departamento de Cochabamba, Bolivia. The single known specimen (CET A501) is a female having a snout–vent length of 35.8 mm. In the diagnosis, De la Riva (1992:19) wrote: "*Gastrotheca lauzuricae* differs from all of the other species of *Gastrotheca* by the presence of bright blue spots on the dorsum and flanks" [translation from Spanish].

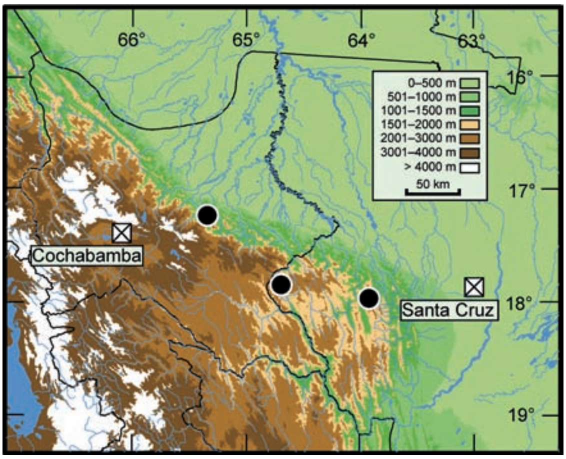

Fig. 12.10 Central Bolivia, showing the localities of known occurrences of *Gastrotheca caeruleomaculata*.

I compared the holotype of *Gastrotheca lauzuricae* with other specimens from Bolivia, as well as with notes on and photographs of the subadult male syntype of *Hylodes caeruleomaculatus*, the female holotype of *Hyla marsupiata*, and the female lectotype of *Nototrema bolivianum*. Morphometrically, these specimens are similar, except the holotype of *G. lauzuricae* is smaller than the other female type specimens. Furthermore, the tibia length in proportion to the snout–vent length is greater and the tympanum diameter in proportion to the eye diameter is smaller in the type specimens of *Hylodes caeruleomaculatus* and *G. lauzuricae* than in the type specimens of *Hyla marsupiata* and *N. bolivianum* (Table 12.4). Of additional specimens from La Siberia, four males have snout–vent lengths of 32.2–35.9 mm ($\bar{x}$ = 34.7), and 35.5–41.2 mm ($\bar{x}$ = 38.4) in four adult females. *G. lauzuricae* is like *Hylodes caeruleomaculatus* in having pale blue spots on the dorsum, and in its various measurements and proportions. Thus I conclude that *G. lauzuricae* De la Riva, 1992, is a junior synonym of *Hylodes caeruleomaculatus* Werner, 1899, since De la Riva overlooked the description of *Hylodes caeruleomaculatus* by Werner nearly 100 years earlier and its subsequent placement in *Nototrema* [= *Gastrotheca*] by Nieden (1923). I suspect that many of the records of *G. marsupiata* in the mountains of eastern Departamento de Cochabamba actually may refer to *G. caeruleomaculata*.

Table 12.4 Measurements and proportions of type specimens for four nominal species

Character	*Hyla marsupiata* MNHN 4877	*Nototrema bolivianum* NMW 16490	*Hylodes caeruleomaculatus* NMW 16496	*Gastrotheca lauzuricae* CET A501
Snout–vent length (SVL)	48.2	42.8	28.8	35.8
Tibia length (TL)	21.6	20.0	14.2	17.9
TL/SVL (%)	44.8	46.7	49.3	50.0
Foot length (FL)	22.2	20.8	12.9	16.6
FL/SVL (%)	46.1	48.6	44.8	46.4
Head length (HL)	14.3	13.9	9.9	12.3
Head width (HW)	16.3	15.3	11.0	14.2
HL/HW (%)	87.7	90.8	90.0	86.7
Interorbital distance (IOD)	5.0	4.9	3.2	3.8
Eyelid width (EW)	4.6	4.4	3.0	3.6
IOD/EW (%)	108.7	111.1	106.7	105.6
Eye diameter (ED)	4.6	4.6	3.8	4.3
Eye–nostril distance (EN)	3.5	3.4	2.9	3.4
ED/EN (%)	131.4	135.3	131.0	126.4
Tympanum diameter (TD)	2.7	2.7	1.9	2.2
TD/ED (%)	58.7	58.7	50.0	51.2
Thumb length (T)	7.2	5.8	3.8	4.5
Third finger length (TF)	15.4	13.5	9.2	11.1
T/TF (%)	46.8	43.0	41.3	40.5

Gastrotheca (*Gastrotheca*) *carinaceps* Duellman, Trueb, and Lehr

Gastrotheca carinaceps Duellman, Trueb, and Lehr, 2006: 596.—Holotype: MUSM 19901 from the vicinity of San Alberto 2200 m, Provincia de Oxapampa, Región de Pasco, Peru.

Diagnosis

In this large species (females to 79.7 mm), the tibia length is more than 55% of the snout–vent length, and is much longer than the foot. The interorbital distance is about twice the width of the upper eyelid. The skin on the dorsum is finely granular, nearly smooth, and lacks transverse ridges; the skin of the head is not co-ossified with the underlying cranial elements. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first and second fingers are equal in length. The discs are much wider than the digits. The fingers are unwebbed; on the foot the webbing extends to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is uniformly green. Markings on the head consist of a pale margin on the upper lip. A pale dorsolateral stripe is absent. The flanks are a uniform green; the venter is pale green.

Gastrotheca carinaceps is like *G. orophylax* in being a uniformly green frog, except *G. orophylax* has a narrow bronze labial stripe, a short bronze supratympanic stripe, and a bronze tympanum; the stripes are absent and the tympanum is green in *G. carinaceps*. *G. orophylax* also differs by having the first finger slightly shorter than the second and a truncate snout in profile, and by lacking the cranial crests that are prominent in *G. carinaceps*. In size and structure, *G. carinaceps* is like *G. monticola* and *G. plumbea*, both of which commonly have pale dorsolateral, labial, and supracloacal stripes. Furthermore, most specimens of *G. monticola* have dark markings dorsally and black spots ventrally, and *G. plumbea* has dark brown flanks. *G. longipes* also is uniformly green (or nearly so), but it differs from *G. carinaceps* in having the fingers about one-fourth webbed and a narrower (± 125%) interorbital distance, and by lacking cranial crests. Superficially, unicolored individuals of *G. aureomaculata* are similar to *G. carinaceps*, but the former differs by having dorsal skin that is more coarsely areolate and a distinctive golden tympanum, and by lacking cranial crests.

Description

The following description is based on two adult females. The body is moderately robust; females attain a snout–vent length of 79.7 mm. The head is wider than long, and as wide as the body. The snout is acutely rounded in dorsal view, and inclined anteroventrally in profile. The canthus rostralis is elevated, straight, and angular in cross-section. The loreal region is concave;

the lips are flared. The top of the head is depressed between the elevated lateral edges of the frontoparietals. The frontoparietals form prominent cranial crests, extending posteriorly to the posterior edge of skull. The interorbital distance is about twice the width of the upper eyelid. The internarial area is flat. The nostrils are protuberant, and are directed anterolaterally well behind the level of the anterior margin of the lower jaw. The diameter of the eye is greater than its distance from the nostril. The tympanum is nearly round, and is separated from the eye by a distance about half again the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately weak, and extends downward from midlength of a dorsolaterally projecting supratympanic crest.

The arm is moderately robust; ulnar tubercles are absent. The hand is large. The fingers are long. The fingers bear moderately large elliptical discs; the width of the disc on the third finger is slightly less than the diameter of the tympanum. The relative lengths of the fingers are I = II < IV < III. The fingers are unwebbed. The subarticular tubercles are moderately large and round; none are bifid. The supernumerary tubercles are moderately large and subconical; they are present only on the proximal segments. The palmar tubercle is low and bifid; the prepollical tubercle is elliptical; the condition of nuptial excrescences is unknown. The hind limb is moderately robust. The tibia length is about 56% of the snout–vent length; the foot length is about 49% of the snout–vent length. A calcar on the heel and tarsal tubercles are absent. An inner tarsal fold is absent. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is flat, ovoid, and barely visible from above. The toes are long. The relative lengths of the toes are I < II < III < V < IV. The toes are about one-third webbed; the webbing formula is $\mathbf{I}2^{+}\text{—}2^{+}\mathbf{II}2\text{—}3^{+}\mathbf{III}2^{+}\text{—}3\mathbf{IV}3\text{—}2^{+}\mathbf{V}$. The subarticular tubercles are moderately large and round; the supernumerary tubercles are large, subconical, and present only on the proximal segments.

The skin on the dorsum of the head, body, and limbs is smooth to finely granulate; the skin on the head is not co-ossified with the underlying cranial elements; the skin on the flanks is areolate; the skin on the throat, belly, and ventral surfaces of the thighs is granular. A pair of moderately large tubercles is present below the cloacal opening. The opening of the pouch is narrowly U-shaped, with the anterior border at the level of the posterior edge of the sacrum. The dentigerous processes of the vomers are slightly inclined posteromedially, and are separated medially between the small round choanae. Each process bears eight or nine teeth.

COLOR IN PRESERVATIVE

All dorsal surfaces—except Fingers I and II, the flanks, the sides of the head, and the anterior and posterior surfaces of thighs—are dark gray. The dorsal surfaces of Fingers I and II are tan. The tympanum is dark brown. The margin of the upper lip is pale gray, with small diffuse pale brown marks extending dorsally onto the lip. The venter is dull grayish brown, with a few small cream spots on the throat. The palmar and plantar surfaces are pale gray.

COLOR IN LIFE

Based on a color photograph (Fig. 12.11), the dorsum is dull green; the margin of the upper lip is greenish white; the tympanum is green. Fingers I and II are tan, with dark brown terminal discs. Of the ventral surfaces, the chest at least is pale green, with white spots. The iris is cream, with reddish-brown reticulations.

MEASUREMENTS

The following measurements (in mm) are those of two females: snout–vent length 74.5, 79.7; tibia length 43.1, 44.0; foot length 37.6, 39.1; head length 25.3, 26.2; head width 27.8, 29.0; interorbital distance 10.1, 11.3; eyelid width 5.3, 5.8; internarial distance 4.9, 4.9; eye diameter 7.3, 8.1; eye–nostril distance 6.7, 7.1; orbit–jaw distance 4.9, 4.9; nostril–jaw distance 6.4–6.6; tympanum diameter 4.1, 5.2; thumb length 14.7, 14.9; third finger length 24.4, 27.0; and width of disc on third finger 3.9, 4.1.

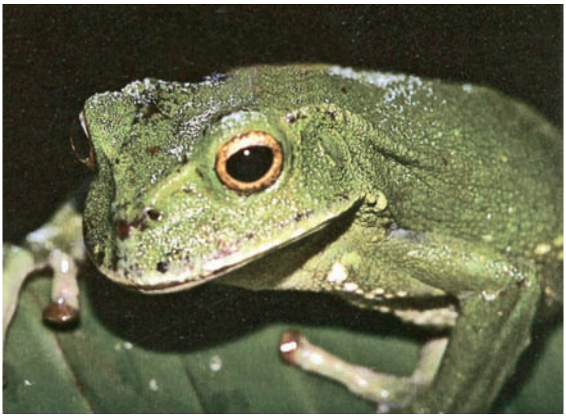

Fig. 12.11 *Gastrotheca carinaceps*, female, Parque Nacional Yanachaga-Chemillén, Pasco, Peru. Photo by H. Plenge; courtesy of E. Lehr.

CRANIAL OSTEOLOGY

The dermal roofing bones are not co-ossified with the overlying skin; the sphenethmoid is sculptured. The nasals broadly articulate medially; their borders are distinct from the sphenethmoid. The frontoparietals have a complete articulation medially; each bears a broad supraorbital flange, and a broad otic flange that does not articulate with the squamosal. A temporal arcade is absent. The carotid canal is open. The preorbital process is not separated by a notch from the facial process of the maxilla; there is a broad postorbital process on the maxilla. The head of the squamosal has a broad crest; the zygomatic ramus extends to the maxilla; the otic ramus completely articulates with and moderately overlaps the ossified crista parotica. An auxiliary dorsal ramus of the squamosal is absent. The parasphenoid has a short posteromedian process; the cultriform process terminates at midlevel of the neopalatines. The parasphenoid alae are elongate, and articulate with the pterygoids. The neopalatines are massive, widely separated medially, and form the posterior margins of the choanae; the ventral ridge of the neopalatine is smooth. The pterygoid articulates with the squamosal; the median ramus of the pterygoid is expanded medially; an auxiliary dorsal ramus is absent.

Life History

Neither female contains eggs in the brood pouch, and the paratype is devoid of ovarian eggs. Presumably the eggs of *Gastrotheca carinaceps* undergo direct development and hatch as froglets.

Distribution and Ecology

This species is known only from the type locality, at an elevation of 2200 m on the Amazonian slopes of the Andes in central Peru (Fig. 12.12).

Conservation Status

The species is recognized as Data Deficient in the IUCN Red List. As noted by Duellman et al. (2006), the two known specimens were found in humid montane forest within the Parque Nacional Yanachaga; therefore the species occurs in a protected region that encompasses forested slopes of the Andes.

Etymology

According to the original description (Duellman et al., 2006), the specific name is derived from the Latin *carina*, meaning "keel" or "ridge," and the Greek *kephale*, meaning "head." The name is a noun in apposition and refers to the prominent cranial crests formed by the elevated lateral edges of the frontoparietals and otic rami of the squamosals.

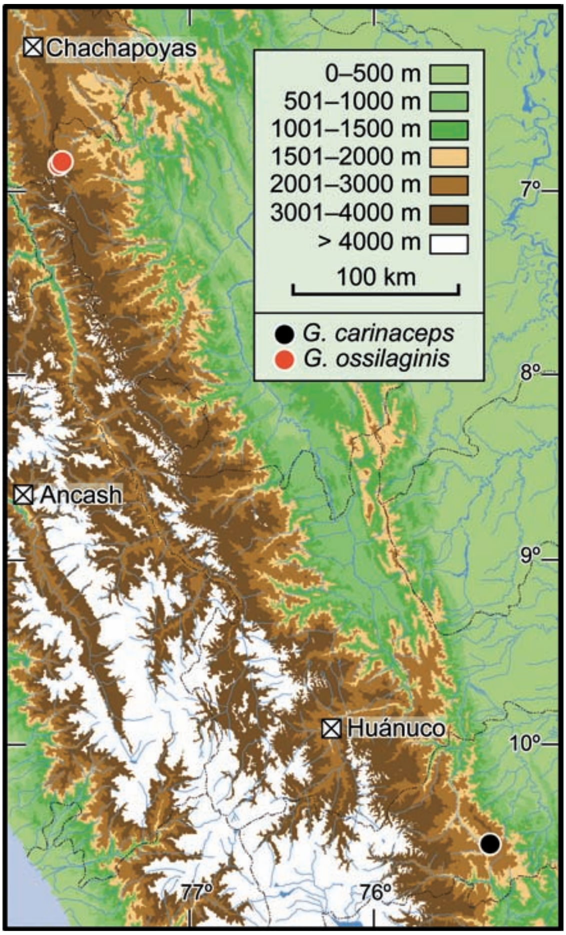

Fig. 12.12 Andean region of central and northern Peru, showing the localities of known occurrences of *Gastrotheca carinaceps* and *G. ossilaginis*.

Remarks

This large frog is unlike any other species in the Peruvian Andes. It is placed in the direct-developing species in the subgenus *Gastrotheca* as a "best guess."

Gastrotheca (Gastrotheca) christiani Laurent

Gastrotheca christiani Laurent, 1967:354.—Holotype: FML 1369 from Monumento Ruta Valle Grande, 50 km NW Calilegua, Provincia de Jujuy, Argentina.

Gastrotheca (Opisthodelphys) christiani—Dubois, 1987:31.

Diagnosis

In this moderately small species, in which females reach a snout–vent length of 39.1 mm, the tibia length is less than 50% of the snout–vent length, and is barely (if at all) longer than the foot. The interorbital distance is noticeably wider than the upper eyelid. The skin on the dorsum is tuberculate, and lacks transverse ridges; the skin on the head is not co-ossified with the underlying cranial elements. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is shorter than the second. The fingers bear subtruncate discs that are much wider than the digits proximal to the discs. The fingers are webbed basally; the webbing extends maximally to a point proximal to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is tan, with narrow brown paravertebral markings and a median longitudinal mark posteriorly; these markings are confluent or not in the sacral region. Markings on the head consist of a dark canthal stripe and (usually) a dark interocular bar. A pale dorsolateral stripe is absent; the flanks are brown, with small cream spots; the venter is uniformly cream.

Gastrotheca christiani differs from other southern Andean *Gastrotheca* (except *G. chrysosticta*, *gracilis*, and *ochoai*) by having tuberculate skin on the dorsum. The dorsal skin is highly tuberculate in *G. christiani* and *G. gracilis*, compared with having scattered large tubercles in *G. chrysosticta* and scattered small tubercles in *G. ochoai*. *G. christiani* is like *G. chrysosticta* in having a dorsal color pattern consisting of a pair of longitudinal dark markings, as contrasted to three longitudinal markings in *G. gracilis* and dark flecks in *G. ochoai*. *G. christiani* also differs from *G. gracilis* in having distinct dark brown canthal and postorbital bars; these are diffuse in *G. gracilis*. In *G. gracilis* the flanks are cream with brown mottling, compared with brown with cream spots in *G. christiani*. *G. christiani* and *G. chrysosticta* are similar in gross color pattern, but the latter differs by having white mottling on the upper lip and a truncate snout in profile.

Description

The following description is based on 15 specimens. The body is robust; males attain a snout–vent length of 38.0 mm, and 39.1 mm in females. The head is wider than long, and not quite as wide as the body. The snout is acutely rounded in dorsal view, and is bluntly rounded in profile. The canthus rostralis is nearly straight. and is rounded in cross-section. The loreal region is slightly concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 145% of the width of the upper eyelid. The internarial area is flat to slightly convex. The nostrils are barely protuberant, and are directed laterally at the anterior terminus of the canthus rostralis. The diameter of the eye is about equal to its distance from the nostril, and is about twice its distance from the margin of the jaw. The tympanum is broadly ovoid vertically, and is separated from the eye by a distance about 1.5 times the length of the tympanum. The tympanic annulus is distinct and smooth; the upper edge of the tympanum is obscured by a thin tubercular supratympanic fold extending from the posterior corner of the orbit to a point above the insertion of the arm.

The arm is moderately slender; no more than two low round ulnar tubercles are present distally on the forearm. The hand is small. The fingers are long. The discs are moderately large, broader than long, and subtruncate; the width of the disc on the third finger is about 1.5 times the length of the tympanum. The relative lengths of the fingers are I < II < IV < III. The fingers are webbed basally; the webbing formula for the outer fingers is **II**2^{+}–3^{+}**III**3—3^{-}**IV**. The subarticular tubercles are large and round; none are bifid. The supernumerary tubercles are large and subconical; they are present only on the proximal segments of Fingers II–IV. The palmar tubercle is low and trifid; the prepollical tubercle is elongately elliptical, and lacks nuptial excrescences. The hind limb is moderately slender. The tibia length and foot length each are about 47% of the snout–vent length. Calcars, tarsal tubercles, and tarsal folds are absent. The outer metatarsal tubercle is small and subconical; the inner metatarsal tubercle is elevated, elliptical, and visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. The toes are less than one-third webbed; the webbing formula is **I**2^{+}—2^{-}**II**2—3**III**2½—3½**IV**3½—2**V**. The subarticular tubercles are large and round; the supernumerary tubercles are large, low, and present only on the proximal segments.

The skin on the dorsum and flanks is strongly tuberculate (noticeably less tuberculate in specimens from Salta). The tubercles are low, and are round in cross-section; some of those on the body are elongate; the tubercles on the limbs are lower and less distinct. The skin of the loreal region and lips anterior to the posterior border of the orbit is smooth; the skin on the throat, belly, and ventral surfaces of the thighs and upper arms is strongly granular; the other ventral surfaces are smooth. Cloacal tubercles and folds are absent. The opening of the brood pouch is narrowly U-shaped, and is narrowest anteriorly and posteriorly; the anterior end is truncate at the level of the posterior edge of the sacrum. The dentigerous processes of the vomers are slightly inclined posteromedially, and are narrowly separated medially between the posterior borders of the small round choanae. Each process bears three to six teeth.

COLOR IN PRESERVATIVE

The dorsum is yellowish tan, brown, or grayish brown, with dark brown markings consisting of narrow irregular paravertebral longitudinal marks extending from either the occiput or the pectoral region to a point posterior to the sacrum. In one individual (FML 2881A) each blotch is fragmented into three longitudinally elliptical spots; in another (FML 2918A) the blotches are fragmented into irregular spots; and in a third (FML 2881B) the blotches are represented by small flecks. A median nape spot or longitudinal mark is present (except in FML 2881B); in those specimens having paravertebral marks, there is a median longitudinal mark posterior to the sacrum. In five individuals the paravertebral marks converge posteriorly and unite with this mark. Most individuals have an irregularly shaped interorbital bar (interrupted in two specimens), terminating on the median edges of the eyelids. The tip of the snout and margin of the upper lip are dark brown in specimens from Jujuy; in those from Salta the margin of the upper lip is creamy white, mottled with brown. A narrow dark brown canthal stripe is present; a broad dark brown postorbital stripe (absent in FML 2281B) passes along the supratympanic fold and through the tympanum to midflank, where its borders are highly irregular. The rest of the flank is colored like the dorsum, but with round cream spots. The dorsal surfaces of the limbs are yellowish tan, brown, or grayish brown, with dark brown irregular transverse bars (absent in FML 2881B). There are bars on each limb segment: none or one on the upper arm, two on the forearm, one on the wrist, three to four on the thigh, two to four on the shank, and two to four on the tarsus. The width of the bars varies from about half to equal to the width of the interspaces. Small brown spots are present on the dorsal surfaces of the two outer fingers and toes. The anterior surfaces of the thighs are colored like the dorsal surfaces; the posterior surfaces of the thighs are either pale brown with irregular dark brown markings, or dark brown with small irregular creamy tan spots. The venter is creamy yellow to pale grayish tan. In all but one specimen (FML 1606), diffuse to distinct brown spots are present on the throat, chest, and at least the anterior part of the belly.

COLOR IN LIFE

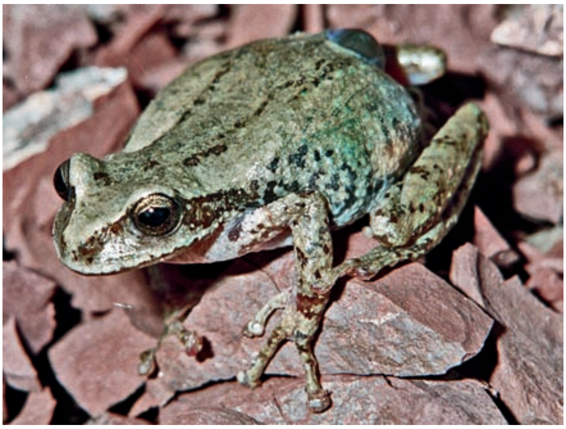

Fig. 12.13 *Gastrotheca christiani*, female, Parque Nacional Calilegua, Jujuy, Argentina. Photo by M. Vaira, KUDA.

Based on photographs, the dorsum is brown to dull green, with parallel black to dark brown paravertebral, canthal, and postorbital stripes (Fig. 12.13). A pale bluish tint is evident in the groin; the venter is cream. The iris is golden yellow, with brown reticulations. Of 10 young born to a brown female, 5 were colored like the mother, and 5 were green (Barrio, 1976).

MEASUREMENTS

Morphometric data for males are summarized in Table 12.5.

CRANIAL OSTEOLOGY

The sphenethmoid is smooth and superficially unsculptured, in contrast to the remainder of the skull table, which bears a semicoarse pit-and-ridge pattern of dermal sculpturing. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially, but lack a distinct supraorbital flange and otic flange. A temporal arcade is absent. The frontoparietal does not extend over the epiotic eminences; the carotid canal is open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are scarcely deflected posteriorly, at an angle less than 10°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for only about 25% of the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is short.

Table 12.5 Univariate statistics for males of *Gastrotheca christiani* and *G. chrysosticta*

	G. christiani ($n = 11$)			*G. chrysosticta* ($n = 16$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	37.4	36.2–38.0	1.29	33.3	30.9–36.1	1.38
Tibia length	18.6	17.9–19.4	0.81	15.3	14.6–15.3	0.36
Foot length	18.2	17.5–18.9	0.71	14.5	13.6–15.2	0.68
Head length	11.7	10.9–12.3	0.28	10.3	9.8–10.9	0.28
Head width	12.9	11.9–13.5	0.58	11.4	10.5–12.0	0.52
Interorbital distance	3.9	3.7–4.1	0.21	3.5	3.3–3.8	0.19
Eyelid width	3.3	2.9–3.6	0.29	3.0	2.6–3.3	0.24
Internarial distance	2.6	2.4–2.8	0.12	2.2	2.0–2.3	0.10
Eye diameter	3.5	3.3–3.8	0.18	3.3	3.1–3.5	0.14
Eye–nostril distance	3.3	3.1–3.4	0.10	2.9	2.8–3.0	0.09
Orbit–jaw distance	1.3	1.0–1.5	0.17	1.1	0.9–1.3	0.14
Nostril–jaw distance	2.2	2.0–2.5	0.25	1.9	1.5–2.1	0.24
Tympanum diameter	1.7	1.5–1.8	0.16	1.7	1.5–1.9	0.17
Thumb length	6.2	5.8–6.5	0.39	5.4	5.0–5.8	0.32
Third finger length	11.7	11.2–12.3	0.61	10.7	9.5–11.3	0.59
Disc width	1.9	1.5–2.4	0.69	2.0	1.5–2.6	0.71

The maxilla lacks a distinct postorbital process, as well as an articulation with the slender zygomatic ramus of the squamosal. The head of the squamosal lacks a crest; the narrow otic plate articulates marginally with the crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in size, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are widely separated medially, and are smooth ventrally. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal and the postorbital process of the maxilla via a long acuminate recurved process on the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located between the middle quadrants of the choanae.

Life History

Breeding occurs during the austral winter and early spring. Males call in April–June and August–November. Males have been reported calling from deep inside crevices in rocks (Vaira et al., 2011). In September 1977, males were calling when the air temperature was −4°C and snow was falling (E. O. Lavilla, pers. comm.). Brooding females have been found in October–December (Barrio, 1976; Laurent et al., 1986). The eggs undergo direct development. Barrio (1976) recorded the birth of 6–10 young and up to 14 eggs each in the pouches of 10 individuals. Eleven brooding females (FML 1841, 2117) having snout–vent lengths of 35.5–39.3 mm contained 10–16 eggs ($\bar{x} = 12.5$) in the pouches. Those eggs in early stages of development were 5.4–5.7 mm ($\bar{x} = 5.55$, $n = 4$) in diameter. One individual collected on 8 December 1972 had 11 fully formed froglets with snout–vent lengths of 9.8–10.0 mm ($\bar{x} = 9.91$). According to Barrio (1976), the duration of brooding is at least 60 days. Laurent et al. (1986) described the parturition of 10 young from the pouch of a female 38.1 mm in snout–vent length, collected on 20 October. Birth commenced on 6 December and lasted 48 hours, 25 minutes. The first five young were expelled from the pouch; subsequently a pair of epithelial sacs came out of the pouch, and the young emerged from the sacs. After parturition the female removed the sacs by using the fourth toe on each foot.

Advertisement Call

Laurent et al. (1986) reported calling males, but they did not describe the call. The advertisement call was described in detail by Vaira et al. (2011), based on recordings made at temperatures of 18°C and 11.5°C on 14 August and 2 September 1995, respectively, at Abra Colorado, Jujuy, Argentina. Although there was no designation of the number of calls analyzed, the statistics for their recordings were a call duration of 1213–1402 milliseconds ($\bar{x} = 1299.2 \pm 77.7$), with the calls containing 47–54 regularly repeated short pulses ($\bar{x} = 50.3 \pm 2.8$). The intervals between calls were 1506–2058 milliseconds ($\bar{x} = 1748 \pm 272.2$). The dominant frequency was 1800–2020.8 Hz ($\bar{x} = 1910.6 \pm 70.9$), and the pulse rate was 38.5–38.8 pulses per second ($\bar{x} = 38.6 \pm 0.1$).

Distribution and Ecology

This species is known only from elevations of 1550–2600 m in the Sierra de Callilegua, Provincia de Jujuy, and elevations of 1550–1600 m in the Sierra de Porongal, Provincia de Salta, Argentina (Fig. 12.14). In the Sierra de Callilegua, *Gastrotheca christiani* inhabits upper montane evergreen forest dominated by *Alnus acuminata*, *Podocarpus parlatorei*, and *Polylepis australis* up to an elevation of 1700 m (Laurent and Terán, 1981). The frogs inhabit holes and cracks in rocky cliffs; others have been found under rocks and moss, and one was in a cavity in a tree trunk.

Conservation Status

Although the species occurs in a protected area, the Parque Nacional Callilegua, it is listed as Threatened in the IUCN Red List because of habitat loss throughout much of its rather restricted range in the Yungas on the Andean slopes. For example, Vaira (2003) reported on the mass extirpation of a breeding aggregation near the Parque Nacional Callilegua. The species has not been observed since 1995 (Akmentins et al., 2012).

Etymology

The specific name *christiani* is a patronym for Christian Halloy, who collected the holotype.

Remarks

Minor differences exist between specimens from the provinces of Salta and Jujuy in Argentina. Those from Jujuy have dorsal skin that is more tuberculate, in addition to a dark brown margin to the lower lip, compared with the lip having a white margin mottled with brown in specimens from Salta.

Vaira et al. (2011) noted two kinds of calls emitted by male *Gastrotheca christiani*, and they described one as an aggressive or territorial call, following Sinsch and Joermann's (1989) designation of a call these two authors witnessed in *G. marsupiata*. The territorial call in *G. christiani* consists of a long note, much like the advertisement call, followed by one or two short notes. Vaira et al. (2011) stated that the first note has a duration of 1300–1640 milliseconds, with 35–50 pulses and a dominant frequency of 1740 Hz.

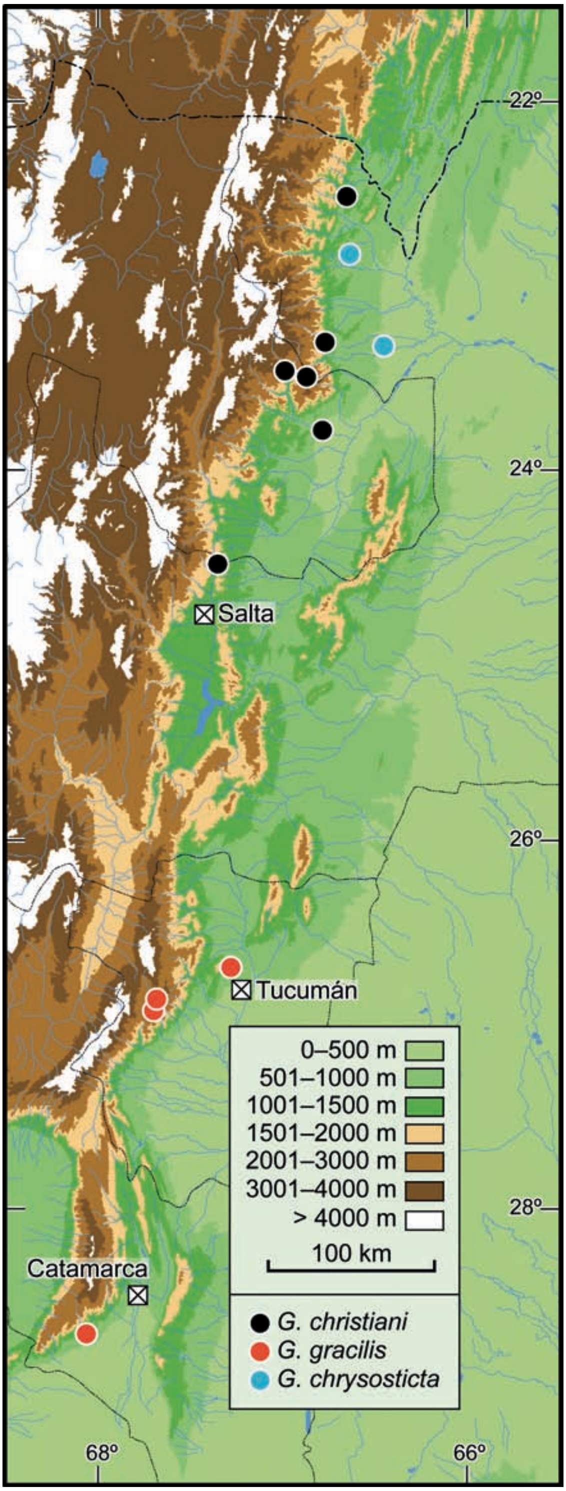

Fig. 12.14 Andean region of northwestern Argentina, showing the localities of known occurrences of *Gastrotheca christiani*, *chrysosticta*, and *gracilis*.

Gastrotheca (*Gastrotheca*) *chrysosticta* Laurent

Gastrotheca chrysosticta Laurent, 1976:58.—Holotype: FML 2098 from Palca de San Martín, Serranía de Porongal, Departamento de Santa Victoria, Provincia de Salta, Argentina.

Gastrotheca (*Gastrotheca*) *chrysosticta*—Dubois, 1987:32.

Diagnosis

In this moderately small species, females attain a snout–vent length of 36.2 mm. The tibia length is less than 50% of the snout–vent length, and is slightly longer than foot. The interorbital distance is slightly greater than the width of the upper eyelid. The skin on the dorsum is smooth, with scattered tubercles, and lacks transverse ridges; the skin on the head is not co-ossified with the underlying cranial elements. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is shorter than the second. The fingers have subtruncate discs that are much wider than digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends maximally to a point proximal to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is tan, with a narrow brown middorsal line bifurcating in the scapular region and uniting postsacrally. Markings on the head consist of a dark canthal stripe and an interocular bar, the latter usually connected to the middorsal mark on the body. A pale dorsolateral stripe is absent. The flanks are uniformly dark brown; the venter is creamy tan, with brown spots.

Gastrotheca chrysosticta differs from other southern Andean *Gastrotheca* (except *G. christiani*, *gracilis*, and *ochoai*) by having tubercular skin on the dorsum. The dorsal skin is highly tuberculate in *G. christiani* and *G. gracilis*, whereas the tubercles are low, round, and scattered on a smooth dorsum in *G. chrysosticta*; they are small and scattered in *G. ochoai*. *G. chrysosticta* differs from all of these species by having a snout that is truncate in profile, instead of round. The species is like *G. christiani* in having a dorsal pattern consisting of two longitudinal dark marks and distinct canthal and postorbital dark bars. It differs from *G. christiani* by being smaller in size and having uniformly dark flanks, instead of cream spots on brown flanks.

Description

The following description is based on 23 specimens. The body is robust; males attain a snout–vent length of 30.9 mm, and 36.2 mm in females. The head is slightly wider than long, and as wide as body. The snout is broadly rounded with a truncate tip in dorsal view, and is truncate in profile. The canthus rostralis is curved, and is rounded in cross-section. The loreal region is slightly concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 120% of the width of the upper eyelid. The internarial area is flat. The nostrils are slightly protuberant, and are directed anterolaterally at the anterior terminus of the canthus rostralis. The diameter of the eye is slightly greater than its distance from the nostril, and is thrice its distance from the margin of the jaw. The tympanum is round, with a distinct smooth tympanic annulus; it is separated from the eye by a distance slightly greater than the length of the tympanum. The upper edge of the tympanum is obscured by a thin tubercular supratympanic fold extending from the posterior corner of the orbit to a point above the insertion of the arm.

The arm is moderately slender; ulnar tubercles are absent. The hand is small. The fingers are slender, moderately long, and unwebbed. The discs are moderately large, and are laterally elliptical; the width of the disc on the third finger is equal to the diameter of the tympanum. The relative lengths of the fingers are I < II < IV < III. The subarticular tubercles are large, low, and round; none are bifid. The supernumerary tubercles are large, subconical, and numerous on the proximal segments of Fingers II–IV. The palmar tubercle is small, elevated, and distinctly trifid; the prepollical tubercle is broadly elliptical; the thumb in males bears pale brown nuptial excrescences. The hind limb is robust. The tibia length is about 46% of the snout–vent length; the foot length is about 45% of the snout–vent length. Calcars and tarsal tubercles are absent. The inner tarsal fold is curved on the distal one-third of the tarsus. The outer metatarsal tubercle is small and subconical; the inner metatarsal tubercle is elliptical, elevated, and visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. Webbing is absent between the inner toes, and is basal between the outer toes; the webbing formula is **III**2½—3½**IV**3½—2**V**. The subarticular tubercles are moderately large and subconical; the supernumerary tubercles are small, subconical, and present only on the proximal segments.

The skin on the dorsum of the head, body, and limbs is smooth, with or without rounded tubercles; the skin on the flanks is areolate; the skin on the throat, belly, and proximal posteroventral surfaces of the thighs is granular. Usually two pairs of small tubercles border the cloacal opening ventrally. The opening of the brood pouch is narrowly U-shaped, with the anterior border at the level of the sacrum. The dentigerous processes of the vomers are slightly curved, inclined posteromedially, and narrowly separated medially just posterior to the posterior margins of the small elliptical choanae. Each process bears three or four teeth.

COLOR IN PRESERVATIVE

The dorsum is pale brown to grayish brown, with dark brown markings consisting of a pair of irregular longitudinal dark marks usually interconnected anteriorly and posteriorly (marks fragmented in three specimens). A broad interorbital bar terminates on the middle of the upper eyelids. In 80% of the specimens, there is a posteromedian stripe from the interorbital bar; in all but three specimens, this stripe is continuous with the anterior part of the interconnected paravertebral marks. In all but eight specimens, 3–22 small white spots ($\bar{x} = 10.2$) are present on the dorsum. A dark brown canthal stripe is present (discontinuous in two specimens). Except in one specimen, a broad dark brown postorbital stripe passes through the tympanum and terminates on the midflank (13 specimens) or in the groin (10 specimens). The margin of the upper lip is mottled creamy white and dark brown. Transverse dark brown bars on the limbs are about as wide as the interspaces. There are bars on each limb segment: none or one on the upper arm, two to three on the forearm, one on the wrist, three to five on the thigh, three to four on the shank, and two to three on the tarsus. Small brown spots are present on the dorsal surfaces of the two outer fingers and the toes. The anterior surfaces of the thighs are colored like the dorsal surfaces; the posterior surfaces of the thighs are pale tan, with irregular brown mottling; there is a brown patch in the cloacal region; two or three small white tubercles are present lateral to the midline on the proximal posteroventral edge of each thigh. The venter is pale creamy tan, with brown spots thinly to heavily dispersed on the chest and belly. The throats of calling males are dark grayish brown, with small cream flecks.

COLOR IN LIFE

A color photograph (Fig. 12.15) reveals that the dorsum is tan, with paravertebral, canthal, and postorbital stripes. A short brown middorsal stripe is connected to the interorbital bar. The limbs have narrow dark brown to black transverse bars, with green flecks. The iris is brown and gold.

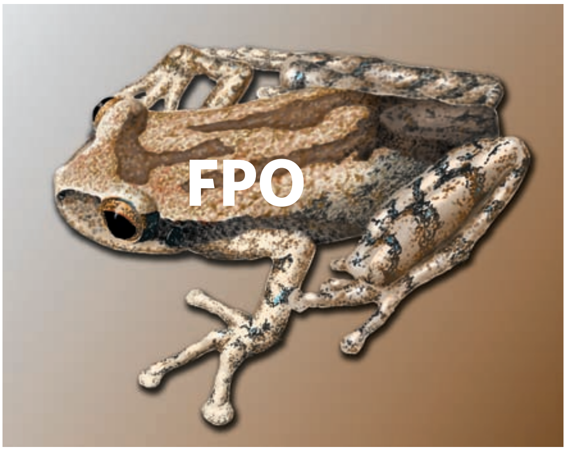

Fig. 12.15 *Gastrotheca chrysosticta*, male, Finca Arazayal, Salta, Argentina. Drawing by L. Trueb, based on a photo provided by R. F. Laurent.

MEASUREMENTS

The measurements for 16 males are summarized in Table 12.5. A single adult female has a snout–vent length of 38.0 mm.

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous coarse pit-and-ridge pattern. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the articulation of the nasal with the anterolateral margin of the frontoparietal is unclear. The frontoparietals have a complete articulation medially, but lack a distinct supraorbital flange and otic flange. A temporal arcade is absent. The frontoparietal does not extend over the epiotic eminences; the carotid canal is open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are scarcely deflected posteriorly, at an angle less than 10°. The premaxillae lack long spinous medial processes. The preorbital process of the pars facialis of the maxilla is visible; the maxilla articulates with the dorsally adjacent nasal for only about 25% of the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The maxilla lacks a distinct postorbital process, as well as an articulation with the slender zygomatic ramus of the squamosal. The head of the squamosal has a narrow crest; the narrow otic plate articulates marginally with the crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in size, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has a blunt terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are widely separated medially, and are smooth ventrally. The pterygoid lacks a dorsal process on its anterior ramus, and does not articulate with either the zygomatic ramus of the squamosal or the maxilla. The vomers bear moderate-sized dentigerous processes located between the posterior quadrants of the choanae.

Life History

Breeding occurs late in the austral winter and spring. Males call from trees and bushes in August–November, and gravid females were found in September and October. Laurent et al. (1986) provided information on reproduction. A gravid female having a snout–vent length of 38 mm that was found in a bromeliad on 13 September gave birth to 33 tadpoles in a terrarium on 28 October. During parturition the female immersed the posterior part of the body, including the opening of the pouch, in water. The first tadpoles swam out of the pouch; subsequently the female stretched the pouch opening by inserting Toes III and IV of both feet into the pouch. Parturition required 25 minutes. Newly born tadpoles have a pair of bell-shaped gills.

Tadpoles

A typical tadpole in Stage 37 (KU 203098) has a body length of 18.5 mm, and a total length of 45.5 mm. In dorsal view the body is broadly ovoid, widest at about two-thirds of its length, and much wider than high. In dorsal view the snout is bluntly rounded; in profile it is rounded. The throat is slightly convex. The interorbital distance is slightly less than one-third the width of the head at the level of the orbits. The eyes are small, and are directed dorsolaterally. The nostrils are much closer to the eyes than to the tip of the snout. The spiracle is attached throughout its length to the body, directed posteriorly at a point about three-fifths the length of the body, and is sinistral to the midline. The cloacal tube is dextral and conical, with a transverse opening. The caudal musculature is moderately robust, and gradually tapers to a tip just short of the rounded tip of the tail. The dorsal fin arises gradually from the body; at midlength of the tail the fins are about equal in height, and are equal to the height of the caudal musculature. The dorsum of the body is brown; the belly is transparent; the caudal musculature is cream; the caudal fins are translucent, with scattered brown flecks.

The width of the oral disc is equal to about one-half of the body; the disc is bordered by two alternating rows of short conical papillae laterally and one row ventrally. The two upper and three lower rows of labial teeth are about equal in length; the first lower row is narrowly interrupted medially. The jaw sheaths are moderately slender, and bear short blunt serrations. The upper sheath is broadly arch-shaped, with moderate alae; the lower sheath is broadly V-shaped.

Advertisement Call

Although Laurent et al. (1986) reported calling males, they did not describe the call.

Distribution and Ecology

This species has a discontinuous distribution in the northern part of the Sierras Subandinas in the Provincia de Salta, Argentina (Fig. 12.14). In addition to the localities from which I have examined specimens, the species is known from Río Pinal and Quebrada La Toma in the Sierra de Metán, Provincia de Salta, Argentina (Laurent et al., 1986). In the Sierra de las Pavas, *Gastrotheca chrysosticta* occurs in subtropical forest at elevations of 600–700 m, whereas in the Sierra de Metán and the Sierra de Porongal, it occurs at elevations of 1200–1800 m in montane forest characterized by *Alnus* and *Podocarpus*. Adults inhabit holes in trees and arboreal bromeliads. De la Riva et al. (2000) and Köhler (2000) noted that this species might occur in the Yungas in Departamento de Tarija, Bolivia, just north of its known distribution in Argentina.

Conservation Status

In the IUCN Red List, *Gastrotheca chrysosticta* is categorized as Vulnerable because its distribution is severely fragmented, and because there is continuing decline in the extent and quality of its forest habitat on the Andean slopes in northern Argentina. Some populations are protected in the Parque Nacional Baritú in Argentina.

Etymology

The specific name is derived from the Greek *chrysos*, meaning "gold," and the Greek *stiktos*, meaning "spotted." The name alludes to the golden-yellow spots on the dorsum of some individuals.

Remarks

Laurent et al. (1986) illustrated the dorsal color patterns of 12 individuals and noted morphometric differences among samples from three localities.

Gastrotheca (*Gastrotheca*) *excubitor* Duellman and Fritts

Gastrotheca excubitor Duellman and Fritts, 1972:23.—Holotype: KU 139194 from the northern slope of Abra "Acjanaco" [= Acanacu], 3370 m, 31 km [by road] NNE Paucartambo, Región de "Cuzco" [= Cusco], Peru.

Gastrotheca (*Opisthodelphys*) *excubitor*—Dubois, 1987:31.

Diagnosis

Adults of this moderately small species attain a snout–vent length of 42 mm. The tibia length is less than 50% of the snout–vent length, and is about as long as foot. The interorbital distance is noticeably greater than the width of the upper eyelid. The skin on the dorsum is smooth or granular, not co-ossified with skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is granular. The first finger is shorter than the second finger. The discs on the fingers are slightly wider than the digits. The fingers are unwebbed; on the foot the webbing extends maximally to a point proximal to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is gray, red, or tan, with a darker large middorsal mark or paravertebral marks. Markings on the head usually consisting of a pale labial stripe, dark canthal stripe, and dark interocular mark, with the latter usually connected to a middorsal mark on the body. A pale dorsolateral stripe is absent. The flanks are pale, with dark spots or flecks; the venter is creamy tan, with dark flecks.

Gastrotheca excubitor has ben confused with *G. nebulanastes*, which has a coarsely granular dorsum in contrast to the smooth dorsum in *G excubitor*. Other structural differences include relative lengths of the first and second fingers (first equal to or shorter than the second in *G. excubitor*, and longer than the second in *G. nebulanastes*). A weak inner tarsal fold is present on the distal half of the tarsus in *G. excubitor* is absent in *G. nebulanastes*. The toes are about one-third webbed in *G. excubitor*, in contrast to only basal webbing in *G. nebulanastes*. The two species also differ in coloration. A dark canthal stripe and pale labial stripe are present in *G. excubitor* but are absent in *G. nebulanastes*, which has dark brown vertical bars on the anterior surfaces of the thighs, in contrast these surfaces being either uniformly tan or tan with brown mottling in *G. excubitor*.

Gastrotheca excubitor differs from all other species (except *G. gracilis* and *G. griswoldi*) by having a dark interorbital bar that is usually connected to the markings on the dorsum of the body. In *G. gracilis* the interorbital bar is connected to a middorsal stripe. In *G. griswoldi* the dorsal markings on the body are narrow and divergent, whereas in *G. excubitor* they are usually in the form of paravertebral marks. Two species in the southern Andes, *G. antoniiochoai* and *G. zeugocystis*, differ from all others by having paired lateral brood pouches. *G. excubitor* differs further from these species by having the webbing extending at least to the antepenultimate subarticular tubercles on the fifth toe, whereas the webbing is basal in *G. antoniiochoai* and *G. zeugocystis*. *G. excubitor* also differs from these two species and other species in the southern Andes by having a much broader interorbital distance, more than 150% of the width of the upper eyelid.

Description

The following description is based on 112 specimens. The body is robust; males and females attain a snout–vent length of 42 mm. The head is slightly wider than long. The snout is bluntly rounded in dorsal view and in profile; it extends slightly beyond the margin of the lower lip. The canthus rostralis is round in cross-section. The loreal region is barely concave; the lips are rounded. The top of the head is flat. The interorbital distance is more than 150% of the width of the upper eyelid. The internarial area is flat. The nostrils are barely protuberant, and are directed dorsolaterally at the terminus of the canthus rostralis at the level of the anterior margin of the lower jaw. The diameter of the eye is slightly greater than its distance from the nostril. The tympanum is round, and is separated from the eye by a distance equal to the length of the tympanum. The tympanic annulus is distinct, and is tubercular anteriorly and ventrally. The supratympanic fold is moderately weak; it extends from the posterior corner of the orbit to a point above the insertion of the forelimb, and obscures the upper part of the tympanum.

The arm is robust. The hand is small. The fingers are short and unwebbed. The discs on the fingers are small and elliptical; the width of the disc on the third finger is equal to the length of the tympanum. The relative lengths of the fingers are I < II < IV < III. The subarticular tubercles are small and round; none are bifid. The supernumerary tubercles are minute, subconical, and numerous on the proximal segments of the fingers. The palmar tubercle is low, flat, and bifid; the prepollical tubercle is elliptical; in breeding males the thumb bears nuptial excrescences. The hind limb is robust. The tibia length is 46.5%–52.4% ($\bar{x} = 48.9$) of the snout–vent length; the foot length is 45.0%–47.6% ($\bar{x} = 46.3$) of the snout–vent length. Calcars are absent on the heels; tarsal tubercles are absent. A weak inner tarsal fold is present on the distal half of the tarsus. The outer metatarsal tubercle is minute and subconical; the inner metatarsal tubercle is small, elliptical, and not visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. The toes are about one-third webbed; the webbing formula is **I**2^{+}—(2^{-}–2) **II**2—3**III**(2^{+}–3)—3^{+}**IV**3^{+}—(2–2½)**V**. The subarticular tubercles are small and round; the supernumerary tubercles are minute, round, and numerous on the proximal segments of the toes.

The skin on the dorsum is smooth (77%) or weakly granular (23%); the skin on the flanks is areolate; the skin on the throat, belly, and ventral surfaces of the thighs is granular; the other surfaces are smooth. Cloacal tubercles and folds are absent. The pouch opening is narrowly U-shaped, with the anterior border at the level of the posterior edge of the sacrum. The vocal sac is large, median, and subgular. The dentigerous processes of the vomers are inclined posteromedially, and are narrowly separated medially between the posterior margins of the small round choanae. Each process bears four or five teeth.

COLOR IN PRESERVATIVE

The dorsum is dull grayish brown or pale brown, with darker brown markings consisting of an interorbital bar (in 84% of the specimens), usually (80%) connected to markings on the dorsum of the body. Dorsal markings consist of continuous (60%) or interrupted (16%) paravertebral markings, or a broad middorsal mark bifurcating posteriorly (24%). Of 115 specimens with continuous paravertebral marks, the marks are fused posteriorly in 12 specimens; posterior bifurcations of broad middorsal marks are separated from the middorsal mark in 21 out of 46 specimens. In addition to dark markings, dark flecks are present in some specimens (11%). The flanks are plain (2%), pale with dark flecks (31%), or pale with dark spots (67%). The anterior surfaces of the thighs are uniformly tan

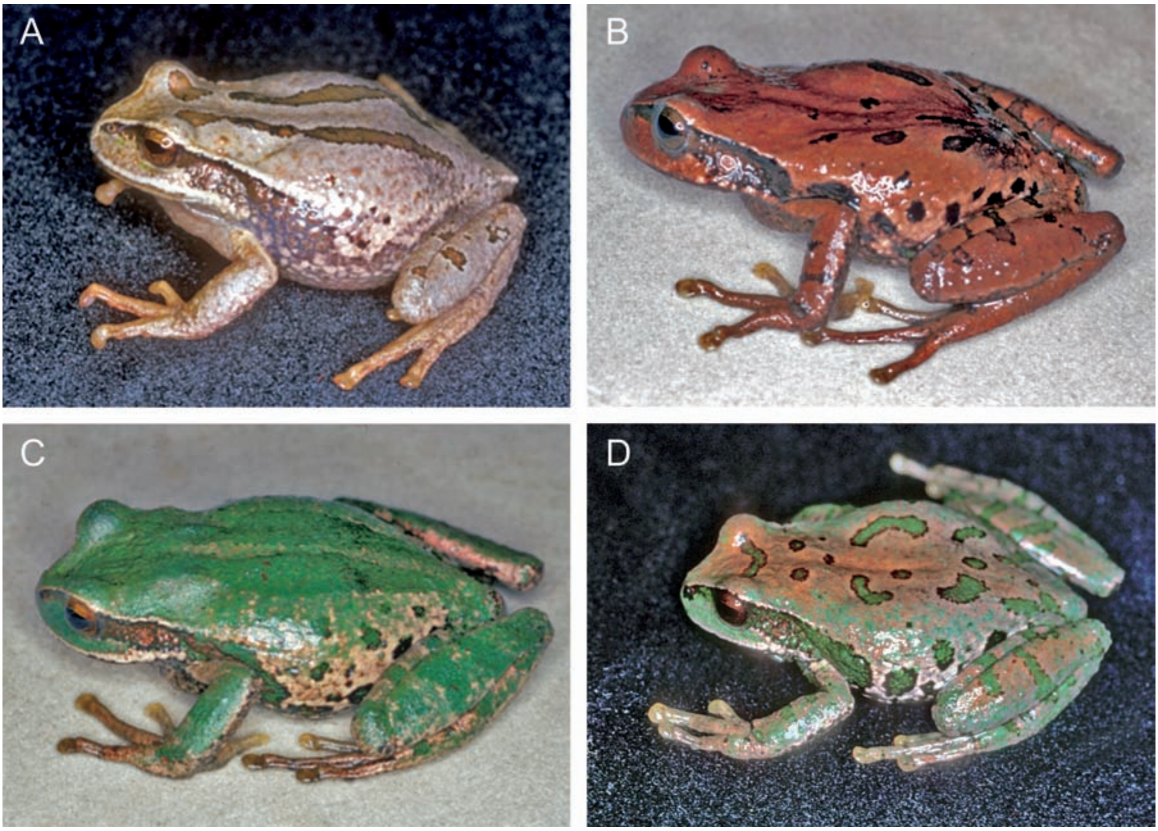

Fig. 12.16 Variation in the coloration of *Gastrotheca excubitor*. A: KU 139200, female, 35.1 mm SVL. B: KU 139195, female, 36.0 mm SVL. C: KU 139198, male, 37.1 mm SVL. D: KU 173193, male, 36.2 mm SVL. All from Abra Acjanaco, Cusco, Peru. Photos by W. E. Duellman.

(27%) or have dark mottling (61%) or bars (12%; all specimens from Buenos Aires). The posterior surfaces of the thighs are tan, with dark spots. The venter is pale creamy tan, with dark flecks in most specimens (83%). The dorsal surfaces of the limbs have distinct transverse bars. The head and limbs have various kinds of stripes: a dark canthal stripe (86%), pale labial stripe (77%), pale supratympanic stripe (91%), pale supracloacal stripe (20%), and pale stripe on the heel (16%).

COLOR IN LIFE

The dorsum is either green with darker green markings, or tan with brown markings. The venter is creamy tan, with or without dark brown flecks; the vocal sac in males is dark grayish brown (Fig. 12.16). The iris is copper, with fine black reticulations. Detailed color notes on living individuals are as follows.

KU 139194–201 from Abra Acjanaco, Región de Cusco, Peru.—One individual has a green dorsum, with darker green marks and bronze-tan flecks; four have a tan dorsum, with bronze-brown markings; one has a grayish tan dorsum, with bronze-brown markings; two have an olive-tan dorsum, with brown markings. The flanks in the green individual are bluish green; the flanks in the tan individuals are creamy tan to pale orange tan, with brown flecks or spots. The venter is pale bronze to pinkish tan (W. E. Duellman field notes, 16 January 1971).

KU 173117–47 from W slope Abra Málaga, 4080 m, Región de Cusco, Peru.—The dorsum is tan, red brown, gray, or green with darker markings (W. E. Duellman field notes, 8 January 1977).

KU 173166–69 from W slope Abra Málaga, 3160 m, Región de Cusco, Peru.—The dorsum is dark brown, tan, or dull green with darker markings; the venter is dusky; the posterior surfaces of the thighs are gray (W. E. Duellman field notes, 11 January 1977).

MEASUREMENTS

The means of many measurements of females are larger than those of males (Table 12.6).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a heterogeneous pattern; the sphenethmoid bears vermiform or ramus ridging; the rest of the skull table has a semicoarse pattern of shallow pits and low rounded ridges. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the fronto-

Table 12.6 Univariate statistics for adults of *Gastrotheca excubitor*

	Males ($n = 73$)			Females ($n = 39$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length**	33.5	28.3–42.5	3.12	35.8	28.7–42.0	3.64
Tibia length**	16.2	12.4–20.9	2.08	17.5	12.4–22.0	2.49
Foot length**	16.8	11.7–20.0	2.27	15.4	11.0–19.7	1.82
Head length	11.4	9.6–14.2	1.01	11.8	9.3–14.3	1.29†
Head width**	12.6	10.5–15.6	1.09	13.4	11.1–15.4	1.37†
Interorbital distance*	4.3	3.2–5.4	0.51	4.1	2.9–5.0	0.43
Eyelid width	2.7	1.8–3.8	0.49	2.9	2.0–3.6	0.44
Internarial distance	1.9	1.3–2.8	0.29	2.1	1.4–2.8	0.34
Eye diameter*	3.2	2.9–4.3	0.46	3.4	2.5–4.3	0.44
Eye–nostril distance	3.0	1.8–3.9	0.51	3.2	1.9–4.3	0.51
Orbit–jaw distance	1.4	0.8–2.8	0.35	1.5	1.0–2.5	0.34
Nostril–jaw distance	2.6	2.0–3.3	0.30	2.6	2.0–3.7	0.37
Tympanum diameter*	1.5	1.0–2.3	0.24	1.6	1.1–2.4	0.29
Thumb length**	6.2	4.7–7.7	0.83	5.9	4.4–7.3	0.71
Third finger length**	11.5	8.2–14.4	1.49	10.7	7.4–13.9	1.29
Disc width	1.5	0.9–2.1	0.31	1.6	1.0–2.8	0.42

*Differences between the means of the sexes are significant (ANOVA, $P = 0.05$).

**Differences between the means of the sexes are significant (ANOVA, $P \le 0.01$).

†Variances are non-homogeneous (Brown-Forsythe test, $P \le 0.05$).

parietal. The frontoparietals have a complete articulation medially, but lack a distinct supraorbital flange, and have only a small otic flange. A temporal arcade is absent. The frontoparietal covers only the anterior epiotic eminence; the carotid canal is partially closed, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for about half the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The maxilla lacks a distinct postorbital process, but articulates with the slender zygomatic ramus of the squamosal. The head of the squamosal has a narrow crest; the narrow otic plate articulates marginally with the crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in size, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are moderately separated medially, and bear a low irregular ridge ventrally. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a long acuminate recurved process on the anterior ramus of the pterygoid. The vomers bear minute dentigerous processes located between the posterior quadrants of the choanae.

Life History

The eggs hatch into froglets. One female having a snout–vent length of 42.0 mm, collected in October, was brooding 22 eggs having diameters of about 6.0 mm each. Twenty-nine females collected in January and February contained 20–22 ovarian eggs ($\bar{x} = 20.9$).

Advertisement Call

The call consists of a single harsh note, followed by two to three short notes. Long notes have a duration of 0.67–1.27 milliseconds ($\bar{x} = 0.99$) and consist of 30–45 pulses ($\bar{x} = 36.9$), whereas the short notes have a duration of 22–32 milliseconds ($\bar{x} = 27.6$). The mean dominant frequency of the long and short notes is about the same: 1739 and 1769 Hz, respectively.

Distribution and Ecology

This species is known from the crests and high Amazonian slopes of the Cordillera Oriental of the Andes (elevations of 3080–4080 m) in Región de Cusco, Peru (Fig. 12.17). Individuals have been found in humid mossy grassland above treeline at Abra Acjanaco (3520 m), Abra Amparaes (3780 m), and Abra Málaga (4080 m). At these sites most individuals were found beneath stones, but some were walking about in deep moss.

Conservation Status

In the IUCN Red List, *Gastrotheca excubitor* is listed as vulnerable; the categorization was justified because the extent of its occurrence was less than 20,000 square kilometers, and its distribution is greatly fragmented.

Etymology

The specific name *excubitor* is Latin, meaning "sentinel," and was used in reference to the outlying Cadena

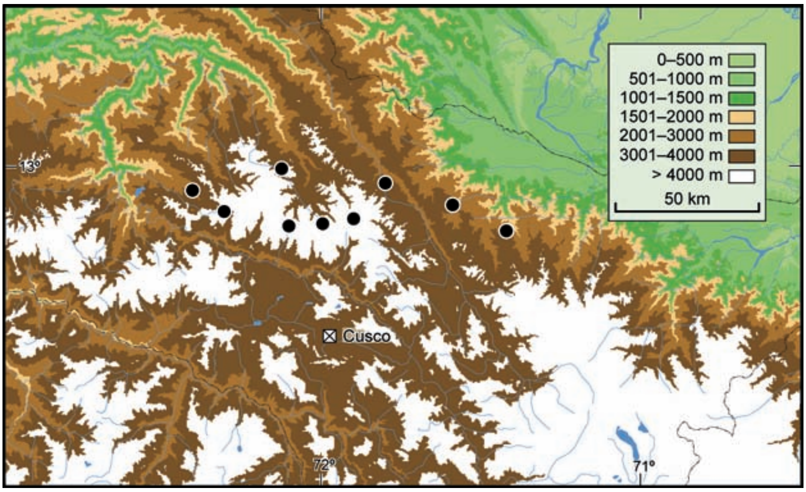

Fig. 12.17 Andean region of Cusco, Peru, showing the localities of known occurrences of *Gastrotheca excubitor*.

de Paucartambo, the type locality (Duellman and Fritts, 1972).

Remarks

There is a general trend from higher to lower elevations toward an increase in dark pigmentation, especially ventrally, and in tuberculation of the skin on the dorsum. Only 6% of the specimens from elevations of more than 4000 m have tuberculate skin on the dorsum; in 23% the skin is areolate, and in 71% it is smooth. In specimens from 3200–3800 m, the skin is tuberculate in 11%, areolate in 22%, and smooth in 67%. Moreover, minor differences exist in coloration (Table 12.7).

Morphometric data on samples from three populations (Abra Málaga, 4080 m; Abra Amparaes, 3780 m; and Abra Acjanaco, 3720 m) were subjected to one-way ANOVA. Sexual dimorphism was evident in some characters in these three populations. In the sample from Abra Acjanaco (26 males, 17 females) significant ($P = \leq 0.05$) differences exist for only two measurements: third finger length and internarial distance.

Comparisons (by sexes) among these populations by one-way ANOVA revealed that among males all measurements (except tympanum diameter) are non-homogeneous, but Brown-Forsythe *F*-tests showed that significant differences exist in all measurements except eye diameter among the three populations. Among females, eight measurements (snout–vent length, tibia length, foot length, head width, eye diameter, tympanum diameter, thumb length, and third finger length) are non-homogeneous, and significant differences exist among all three populations in six measurements (head length, eyelid width, internarial distance, eye–nostril distance, orbit–jaw distance, and width of disc on third finger). A stepwise discriminant function analysis showed no clear distinction among the populations; in a jackknifed five-step model only 63% of the individuals were classified correctly.

Table 12.7 Comparison of color patterns in three populations of *Gastrotheca excubitor* (numbers are percentages)

Character	Abra Málaga $n = 100$	Abra Amparaes $n = 23$	Abra Acjanaco $n = 46$
Canthal stripe	87	100	98
Supratympanic stripe	95	100	98
Labial stripe	68	100	100
Supracloacal stripe	7	26	33
Heel stripe	5	26	22
Venter flecked	77	100	89
Dorsum flecked	10	9	20
Flank pattern			
Uniformly pale	4	0	0
Pale with flecks	59	0	0
Pale with spots	37	100	100

There are no obvious differences in coloration, external features, or morphometrics among the three populations sampled. A distinct genetic difference exists between a specimen (KU 173171) from Abra Amparaes and two individuals (MUSM 26280–81) from Abra Acjanaco (Duellman et al., 2011). Much more extensive phylogeographic analyses most likely will reveal that *Gastrotheca excubitor*, as it is now recognized, consists of two or more cryptic species.

Gastrotheca (*Gastrotheca*) *gracilis* Laurent

Gastrotheca gracilis Laurent, 1969b:146.—Holotype: FML 1389 from La Banderita, Km 51, Ruta Concepción–Andalagá, Provincia de Catamarca, Argentina.

Gastrotheca (*Gastrotheca*) *gracilis*—Dubois, 1987:32.

Diagnosis

Adults of this moderately small species attain a maximum snout–vent length of 44.9 mm. The tibia length is less than 50% of the snout–vent length, and is slightly longer than the foot. The interorbital distance is about equal to the width of the upper eyelid. The skin on the dorsum is tuberculate, and is not co-ossified with the skull; transverse dermal ridges are absent. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is shorter than the second; the discs are slightly wider than the digits. The fingers are unwebbed; on the foot the webbing extending maximally to a point proximal to the antepenultimate subarticular tubercle on the fourth toe and the antepenultimate subarticular tubercle on the fifth toe. The dorsum is tan, with narrow middorsal and paravertebral marks. Markings on the head consist of a pale labial stripe as well as a diffuse dark brown canthal stripe and interorbital bar. A pale dorsolateral stripe is absent. The flanks are cream, with dark brown mottling; the venter is cream, with dark spots or flecks.

Gastrotheca gracilis differs from all other southern Andean *Gastrotheca* (except *G. christiani*, *chrysosticta*, and *ochoai*) by having tuberculate skin on the dorsum. It is larger than any of those species (maximum lengths of males and females, respectively): *G. christiani*, 38.0 and 39.1 mm; *G. chrysosticta*, 30.9 and 36.2 mm; *G. ochoai*, 32.9 and 37.9 mm. In profile the snout is bluntly rounded in three of the species; *G. chris-*

tiani differs by having a truncate snout. The dorsal color pattern consists of three longitudinal marks in *G. gracilis*; two longitudinal marks in *G. christiani* and *G. chrysosticta*; and dark flecks in *G. ochoai*, which also differs from the others by having no dark spots on the venter. *G. gracilis* differs further from *G. chrysosticta* and *G. ochoai* in the texture of the skin on the dorsum: the skin is highly tuberculate in *G. gracilis*, smooth with scattered large tubercles in *G. chrysosticta*, and bears small tubercles in *G. ochoai*. All of these species have distinct dark brown canthal and postorbital bars (except *G. gracilis*) in which the bars are diffuse. The dorsal color pattern is like that of some specimens of *G. marsupiata*, which differs from *G. gracilis* by having the skin on the dorsum smooth or bearing low pustules, and having flanks that are plain or marked with large dark spots (cream mottled with brown in *G. gracilis*).

Description

The following description is based on 15 specimens. The body is moderately robust; males attain a snout–vent length of 41.6 mm, and 44.9 mm in females. The head is wider than long, and as wide as the body. The snout is rounded in dorsal view, and is bluntly rounded in profile. The canthus rostralis is nearly straight, and is rounded in cross-section. The loreal region is concave; the lips are thin and rounded. The top of the head is flat. The interorbital distance is slightly greater than the width of the upper eyelid. The internarial area is flat. The nostrils are barely protuberant, and are directed dorsolaterally below the anterior terminus of the canthus rostralis. The diameter of the eye is about equal to its distance from the nostril, and is slightly more than twice its distance from the margin of the jaw. The tympanum is nearly round, and has a distinct smooth annulus; it is separated from the eye by a distance slightly greater than the length of the tympanum, the upper edge of which is obscured by a moderately heavy tubercular supratympanic fold extending from the posterior corner of the orbit to a point posteroventral to the tympanum.

The arm is moderately slender, and lacks distinct ulnar tubercles. The hand is small. The fingers are long, slender, and unwebbed. The discs are moderately small and ovoid; the width of the disc on the third finger is about equal to the length of the tympanum. The relative lengths of fingers are I < II < IV < III. The subarticular tubercles are moderately large and subconical; none are bifid. The supernumerary tubercles are large and subconical, and are numerous on the proximal segments of the digits. The palmar tubercle is elevated and trifid; the prepollical tubercle is elliptical; the thumb bears brown nuptial excrescences in males. The hind limb is moderately slender. The tibia length is about 50% of the snout–vent length; the foot length is about 47% of the snout–vent length. Calcars and tarsal tubercles are absent; an inner tarsal fold is distinct on the distal one-fourth of the tarsus. The outer metatarsal tubercle is small and rounded; the inner metatarsal tubercle is broadly ovoid, and is visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. The outer toes are webbed basally; the webbing formula is **III**2½—4**IV**3½—2**V**. The subarticular tubercles are moderately large and subconical; the supernumerary tubercles are large, subconical, and present only on the proximal segments of the toes.

The skin on the dorsal surfaces of the body and flanks bears low round tubercles; the skin on the throat, chest, belly, and ventral surfaces of the upper arms and thighs is strongly granular; the other surfaces are smooth. A pair of moderately large tubercles is present below the cloacal opening. The opening of the brood pouch is narrowly U-shaped, with the anterior end rounded at the level of the posterior edge of the sacrum. The dentigerous processes of the vomers are slightly inclined posteromedially, and are narrowly separated medially between the posterior margins of the small round choanae. Each process bears three to five teeth.

COLOR IN PRESERVATIVE

The dorsum is brown, with darker brown markings. Markings on the body consist of three (median and dorsolateral) irregular narrow longitudinal marks that extend from the nape at least to the sacrum. The marks are fragmented into a series of longitudinal spots in 20% of the specimens. A chevron-shaped dark interorbital bar terminates on the middle of each eyelid. The bar is incomplete medially in three specimens, and is connected with the middorsal body mark in one specimen. A diffuse dark brown canthal stripe is present. A diffuse dark brown postorbital stripe passes through the tympanum, and terminates above the insertion of the arm. The margin of the upper lip is creamy white posteriorly from the eye. The flanks are pale cream, mottled with dark brown. Irregular dark brown transverse bars are present on the limbs, with bars on each limb segment: one on the upper arm, two to three on the forearm, one on the wrist, two to three on the thigh, two to three on the shank, and two to three on the tarsus. The outer toes and the fingers are

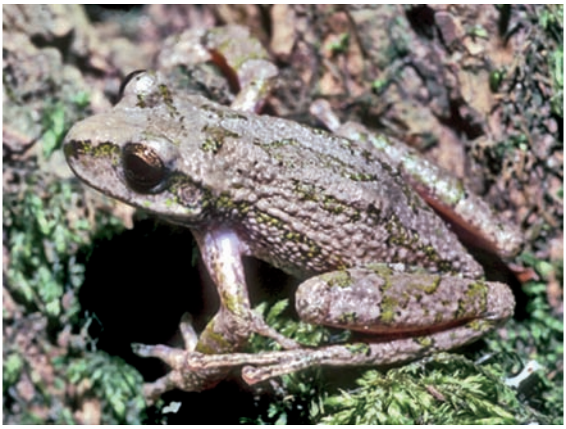

Fig. 12.18 *Gastrotheca gracilis* (KU 160335), male, 30.5 mm SVL, 21 km SSE Tafí del Valle, Tucumán, Argentina. Photo by W. E. Duellman.

marked with dark flecks. The anterior surfaces of the thighs are colored like the dorsal surfaces; the posterior surfaces of the thighs are brown, with cream flecks. The venter is creamy tan, with brown flecks or small spots on the throat, chest, and belly. In calling males, the vocal sac is heavily suffused with brown.

COLOR IN LIFE

The dorsum is dull grayish brown, with green markings (Fig. 12.18). The postorbital stripe is green; the flanks are cream, with dark brown spots. The posterior surfaces of the thighs are pale brown, with cream flecks; the throat and belly are creamy white, with gray flecks; the ventral surfaces of the limbs are pinkish gray. The labial stripe is cream; the tympanum is bronze. The iris is dull bronze, with black flecks (W. E. Duellman field notes, 24 November 1974).

In another individual, the dorsum is coppery brown, with olive-green mottling. The hidden surfaces of the thighs are a dark flesh color; the venter is off white. The iris is copper, with black reticulations (D. C. Cannatella field notes, 19 November 1978).

MEASUREMENTS

Although differences in snout–length between the sexes are not significant, females are larger in several measurements (Table 12.8). The lack of significant differences in snout–vent length and some other measurements probably is an artifact of the small sample size of females.

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a heterogeneous semicoarse pattern of shallow pits and low rounded ridges. The nasals lack a medial articulation; their borders are distinct from the sphenethmoid; posterolaterally, the nasal is separated from the anterolateral margin of the frontoparietal. The frontoparietals are incompletely articulated medially, and lack distinct supraorbital and otic flanges.

Table 12.8 Univariate statistics for adults of *Gastrotheca gracilis*

	Males (n = 17)			Females (n = 3)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	37.7	35.4–41.6	1.91	42.6	39.2–44.9	3.02
Tibia length**	18.6	16.7–21.5	1.21	21.9	19.6–23.8	2.14
Foot length**	17.3	15.8–19.4	1.00	22.0	20.4–23.4	1.52
Head length	12.8	11.2–13.9	0.84	14.0	11.8–15.4	1.91
Head width	13.7	12.3–14.8	0.72	15.0	13.4–15.9	1.42
Interorbital distance**	3.7	3.3–4.9	0.22	4.7	4.5–4.9	0.20
Eyelid width	3.2	2.8–3.6	0.23	3.4	3.2–3.7	0.27
Internarial distance	3.0	2.7–3.4	0.19	3.2	3.1–3.4	0.17
Eye diameter	3.9	3.7–4.3	0.17	4.3	3.9–4.7	0.40
Eye–nostril distance	3.8	3.3–4.3	0.27	4.3	4.0–4.6	0.31
Orbit–jaw distance	1.6	1.1–2.0	0.24	1.8	1.5–2.1	0.31
Nostril–jaw distance	2.5	2.0–2.9	0.27	2.6	2.0–3.0	0.51
Tympanum diameter	2.1	1.7–2.6	0.24	2.2	2.0–2.4	0.20
Thumb length**	5.8	5.1–6.5	0.42	7.2	7.0–7.4	0.21
Third finger length**	11.8	10.5–13.0	0.75	14.2	13.4–14.8	0.71
Disc width**	1.9	1.5–2.4	0.23	2.4	2.3–2.6	0.15

**Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

A temporal arcade is absent. The frontoparietal covers only the anterior epiotic eminence; the condition of the carotid canal could not be assessed. The alary processes of the premaxillae are scarcely deflected posteriorly, at an angle less than 10°. The premaxillae lack long spinous medial processes. The preorbital process of the pars facialis of the maxilla is not evident; the maxilla articulates with the dorsally adjacent nasal for approximately half the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The maxilla lacks a distinct postorbital process, as well as an articulation with the slender zygomatic ramus of the squamosal. The head of the squamosal has a narrow crest; the narrow otic plate articulates marginally with the crista parotica. The nature of the stapedial footplate of the plectrum could not be determined. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are moderately separated medially, and are smooth ventrally. The pterygoid lacks a dorsal process on its anterior ramus, as well as an articulation via this process with the squamosal or maxilla. The vomers bear moderately large dentigerous processes located between the posterior quadrants of the choanae.

Life History

Although males call from May through November, intensive calling begins with the onset of rains in early October. Males call only on rainy or misty nights, from holes in trees or mossy holes in rock cliffs. Gravid females have been found in October–December. Tadpoles have been found on the bottoms of quiet pools in slow-moving rocky streams in November.

One female (FML 1389) having a snout–vent length of 42.9 mm contained 60 eggs, 4.5 mm in diameter each, in the pouch. Another brooding female having a snout–vent length of 39.2 mm contained 62 eggs, also 4.5 mm in diameter each. A female having a snout–vent length of 50 mm produced 68 tadpoles on 11–12 November 1979. According to Laurent et al. (1986), parturition required 30.5 hours and was accomplished while the female was submerged in water, except for her eyes and snout; the last 13 tadpoles (and five undeveloped eggs) were dug out of the pouch by the mother inserting the fourth and fifth toes into the pouch.

Tadpoles

A typical tadpole in Stage 35 (KU 206480) has a body length of 16.0 mm, and a total length of 39.6 mm. In dorsal view the body is ovoid, with the sides nearly parallel, and is slightly wider than high. The snout is bluntly rounded in dorsal view, and is round in profile. The throat is slightly convex. The interorbital distance is about one-third the width of the head at the level of the orbits. The eyes are small, and are directed dorsolaterally. The nostrils are slightly closer to the eyes than to the tip of the snout. The spiracle is attached throughout its length, and is directed posteriorly at a point about midlength of the body; the spiracular opening is below the midline. The cloacal tube is dextral and flask-shaped, with a diagonal opening. The caudal musculature is moderately robust, and gradually tapers to a tip just short of the rounded tip of the tail. The dorsal fin arises gradually from the body. At midlength of the tail the dorsal and ventral fins are about equal in height, and are slightly higher than the caudal musculature. The entire body and tail have moderately dense brown pigment.

The width of the oral disc is equal to about two-fifths the width of the body; the disc is bordered by a single row of short conical papillae anterolaterally, and by two alternating rows laterally and ventrally. There are two upper and three lower rows of labial teeth; the tooth rows are about equal in length; the first lower row is narrowly interrupted medially. The jaw sheaths are moderately slender, and bear fine serrations; the upper sheath is broadly arch-shaped, with short alae; the lower sheath is broadly V-shaped.

Advertisement Call

The call consists of a moderately long note, “crrrrr,” followed by two or three short notes, “tic-tic” (Laurent et al., 1986).

Distribution and Ecology

This species is known from three mountain ranges that are included in the Sierras Pampeanas, to the east of the main range of the Andes in the Provincia de Tucumán and the extreme northern part of the Provincia de Catamarca, Argentina (Fig. 12.14). Localities of occurrence are at elevations of 1260–2000 m in the Sierra de Aconquija, Sierra de San Javier (Cumbres de Tafecillo), and Sierra de Medina. The latter site is in lower montane subtropical deciduous forest dominated by *Parapiptadenia excelsa*, whereas localities in the other ranges are in upper montane evergreen forest dominated by *Alnus acuminata*, *Podocarpus parlatorei*, and *Polylepis australis* (Laurent and Terán, 1981).

Conservation Status

Gastrotheca gracilis is listed as Vulnerable in the IUCN Red List, because its distribution is severely fragmented; there is continuing decline in the extent and quality of its forest habitat in the provinces of Catamarca and Tucumán in Argentina. Some populations are probably protected in the Parque Nacional Los Alisos. Akmentins et al. (2012) reported the rediscovery of this species at two localities; these were the first observations in 20 years.

Etymology

The specific name *gracilis* is Latin, meaning "slender."

Remarks

Laurent et al. (1986) reported that a postpartum female in captivity emitted a call like that of the male advertisement call.

Gastrotheca (*Gastrotheca*) *griswoldi* Shreve

Gastrotheca boliviana griswoldi Shreve, 1941:85.—Holotype: MCZ 24102 from Maraynioc, Región de Junín, Peru.

Gastrotheca marsupiata bifasciata Vellard, 1957:23.—Syntypes: MUSM 129 (3 specimens) from Paccha, near La Oroya, Región de Junín, Peru. Synonymy fide Duellman and Fritts, 1972:21.

Gastrotheca bifasciata bifasciata—Laurent, 1969a:131.

Gastrotheca griswoldi—Duellman and Fritts, 1972:21.

Gastrotheca (*Opisthodelphys*) *griswoldi*—Dubois, 1987:31.

Diagnosis

In this moderately small species (females to 43.5 mm), the tibia length is less than 50% of the snout–vent length, and is about as long as the foot. The interorbital distance is slightly greater than the width of the upper eyelid. The skin on the dorsum is granular, not co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is shorter than the second; the discs are slightly wider than the digits. The fingers are unwebbed; on the toes the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is gray, green, or tan, with darker paravertebral marks. A pale labial stripe usually is present; there is a dark canthal stripe, and a dark interorbital bar that usually is connected to the dark marks on the body. A pale dorsolateral stripe is absent. The flanks are paler than the dorsal ground color, and have dark spots; the venter is creamy tan, with dark flecks.

Gastrotheca griswoldi differs from all other species (except *G. excubitor* and *G. gracilis*) by having a dark interorbital bar that is usually connected medially to the dorsal markings on the body. In *G. griswoldi* the dorsal markings are narrow and divergent, whereas in *G. excubitor* the markings are broad, parallel, and fused in some individuals. In *G. gracilis* the interorbital bar is connected to a middorsal stripe; *G. griswoldi* differs further from these species and from *G. pacchamama* in having a proportionately narrower interorbital width, and shorter hind limbs (tibia length less than foot length).

Description

The following description is based on 54 specimens. The body is robust; the maximum snout–vent length is 40.0 mm in males, and 43.5 mm in females. The head is slightly wider than long, but not as wide as the body. The snout is bluntly rounded in dorsal view and in profile. The canthus rostralis is rounded in cross-section. The loreal region is barely concave; the lips are round. The top of the head is flat. The interorbital distance is about 117% of the width of the upper eyelid. The internarial area is flat. The nostrils are barely protuberant, and are directed dorsolaterally at the terminus of the canthus rostralis at the level of the anterior margin of the lower jaw. The diameter of the eye is equal to its distance from the nostril. The tympanum is round, and is separated from the eye by a distance equal to the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately heavy, and extends from the posterior corner of the orbit to a point above the insertion of the arm.

The arm is robust; a row of low ulnar tubercles is present. The hand is small. The fingers are short and unwebbed. The discs are small and elliptical; the width of the disc on the third finger is equal to the length of the tympanum. The relative lengths of the fingers are I < II < IV < III. The subarticular tubercles are moderately large and round; none are bifid. The supernumerary tubercles are minute, subconical, and numerous proximally on the hand. The palmar tubercle is low, flat, and bifid; the prepollical tubercle is elliptical; in breeding males the thumb bears nuptial excrescences. The hind limb is robust. The tibia length is about 43% of the snout–vent length; the foot length is about 44% of the snout–vent length. The heel lacks a calcar. Tarsal tubercles are absent; the weak inner tarsal fold is curved on the distal two-thirds of the tarsus. The outer metatarsal tubercle is small and subconical; the inner metatarsal tubercle is small, flat, ovoid, and not visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV.

Webbing is absent between the first and second and between the second and third toes; the webbing formula for the outer toes is **IV**(3–3½)—(2–2½)**V**. The subarticular tubercles are moderately large and round; the supernumerary tubercles are minute, subconical, and numerous on the proximal segments of the toes.

The skin on the dorsal surfaces of the head, body, and limbs, on the flanks, and on the belly and ventral surfaces of the thighs is granular. Cloacal folds and tubercles are absent. The opening of the pouch is narrowly U-shaped, with the anterior margin at the posterior edge of the sacrum. The dentigerous processes of the vomers are steeply inclined posteromedially, and are narrowly separated medially at a level slightly posterior to the small round choanae. Each process bears three to five teeth.

COLOR IN PRESERVATIVE

The dorsum is dull tan to gray, with darker markings consisting of an interorbital bar usually (96.4%) connected to markings on the dorsum of the body; usually (82%) these markings are in the form of paravertebral marks. In addition to the paravertebral marks, dark flecks or spots are present in 25% and 7% of the specimens, respectively. The flanks are uniformly pale (4%) or have dark spots (96%). A pale dorsolateral stripe is absent. A pale labial stripe usually (89%) is present; a dark canthal stripe also is present. A pale supracloacal stripe usually (93%) is absent. The anterior surfaces of the thighs are uniformly pale (9%) or pale with dark spots (91%); the posterior surfaces of the thighs are pale, with dark spots. The dorsal surfaces of the shanks are pale, with dark transverse bars. The chest and belly are uniformly pale creamy tan (9%) or usually (91%) have dark flecks. The throat is densely flecked with gray; the ventral surfaces of the limbs are uniformly pale creamy tan.

COLOR IN LIFE

In adults the dorsum is gray or tan, with darker markings (Fig. 12.19). The variation in coloration is evident in the following descriptions of living individuals.

KU 138222–23 from Comas, Región de Junín, Peru.—The dorsum is greenish gray, with dull green blotches and occasional dull red spots; the dorsal surfaces of the limbs are gray, with dull green blotches (T. H. Fritts field notes, 26 September 1968).

KU 139140–50 from Paccha, Región de Junín, Peru.—The dorsum is gray with green markings, tan with brown markings, gray with brown markings, or tan with green markings; some individuals have white spots or yellow flecks. The venter is creamy white, with or without black flecks; the posterior surfaces of the thighs are pinkish tan; the flanks are grayish white, with black spots. The iris is bronze, darkest medially and nearly copper ventrally, with a median horizontal red-brown streak and black reticulations (W. E. Duellman field notes, 22 January 1971).

KU 139152–54 from 14 km SW Paucartambo, Región de Pasco, Peru.—The dorsum is brown with green markings, or tan with brown spots. The venter is creamy white (W. E. Duellman field notes, 23 January 1971).

MEASUREMENTS

Although females are slightly larger than males in overall size, the differences between the means of none of the measurements are significant (Table 12.9).

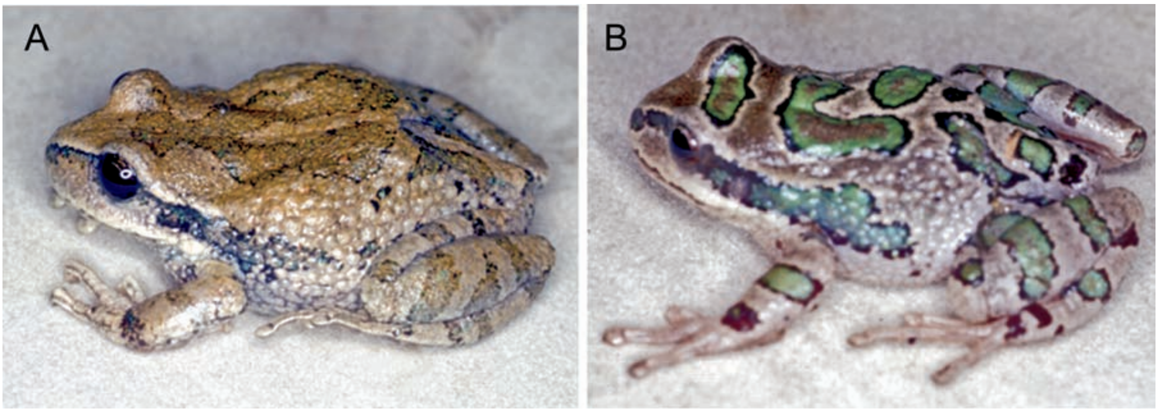

Fig. 12.19 *Gastrotheca griswoldi*. A: KU 139151, female, 42.1 mm SVL, Paccha, Junín, Peru. B: KU 139152, male, 32.8 mm SVL, 14 km SW Paucartambo, Pasco, Peru. Photos by W. E. Duellman.

Table 12.9 Univariate statistics for adults of *Gastrotheca griswoldi*

	Males (n = 20)			Females (n = 34)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	35.1	29.3–40.0	2.56	36.0	29.7–43.5	3.97
Tibia length	15.2	13.2–16.9	1.00	15.6	12.6–19.9	1.57
Foot length	15.6	13.3–16.9	0.93	16.2	12.2–20.3	1.55
Head length	11.3	10.1–12.6	0.73	11.4	8.7–13.4	1.04
Head width	12.6	10.9–13.8	0.77	12.9	10.3–15.6	1.19
Interorbital distance	3.8	2.8–4.6	0.48	3.9	3.0–4.9	0.53
Eyelid width	3.2	2.6–3.7	0.28	3.3	2.7–4.0	0.33
Internarial distance	2.5	2.0–3.8	0.36	2.5	1.9–3.2	0.28
Eye diameter	3.2	2.4–3.9	0.44	3.4	2.5–4.0	0.37
Eye–nostril distance	3.2	2.5–3.9	0.31	3.3	2.7–4.2	0.35
Orbit–jaw distance	1.7	1.2–2.3	0.25	1.7	1.2–2.3	0.35
Nostril–jaw distance	2.5	2.0–3.1	0.38	2.5	1.7–3.2	0.46
Tympanum diameter	1.7	1.2–2.2	0.25	1.8	1.1–2.2	0.22
Thumb length	6.2	5.1–7.5	0.66	5.9	4.9–7.7	0.61
Third finger length	10.6	9.3–11.8	0.65	11.0	8.6–13.4	0.94
Disc width	1.5	1.1–1.8	0.20	1.5	1.2–2.1	0.24

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous vermiform/ramous pattern. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals are incompletely articulated medially, and lack distinct supraorbital and otic flanges. A temporal arcade is absent. The frontoparietal does not extend over the epiotic eminences; the carotid canal is open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are scarcely deflected posteriorly, at an angle less than 10°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for only about 25% of the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The maxilla lacks a distinct postorbital process, as well as an articulation with the slender zygomatic ramus of the squamosal. The head of the squamosal lacks a crest; the narrow otic plate articulates marginally with the crista parotica. The dorsal part of the stapedial footplate is two the three times the size of the ventral portion, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are widely separated medially, and are smooth ventrally. The pterygoid lacks a dorsal process on its anterior ramus, as well as an articulation with either the zygomatic ramus of the squamosal or the maxilla. The vomers bear moderate-sized dentigerous processes located between the posterior quadrants of the choanae.

Life History

The eggs of *Gastrotheca griswoldi* undergo direct development into froglets in the pouch. Six gravid females collected in January, having snout–vent lengths of 36.1–40.5 mm ($\bar{x}$ = 38.1), contained 20–22 eggs ($\bar{x}$ = 21.7) with diameters of 2.6–3.7 mm ($\bar{x}$ = 3.04). Presumed newly metamorphosed young were collected in February; 16 individuals had snout–vent lengths of 14.8–19.5 mm ($\bar{x}$ = 17.0).

Advertisement Call

The call was described by Sinsch and Juraske (2006) as consisting of a single note, with an average of 72 pulses. The duration of the call is flexible, with a mean duration of 2.3 seconds and a mean dominant frequency of 1.98 kHz.

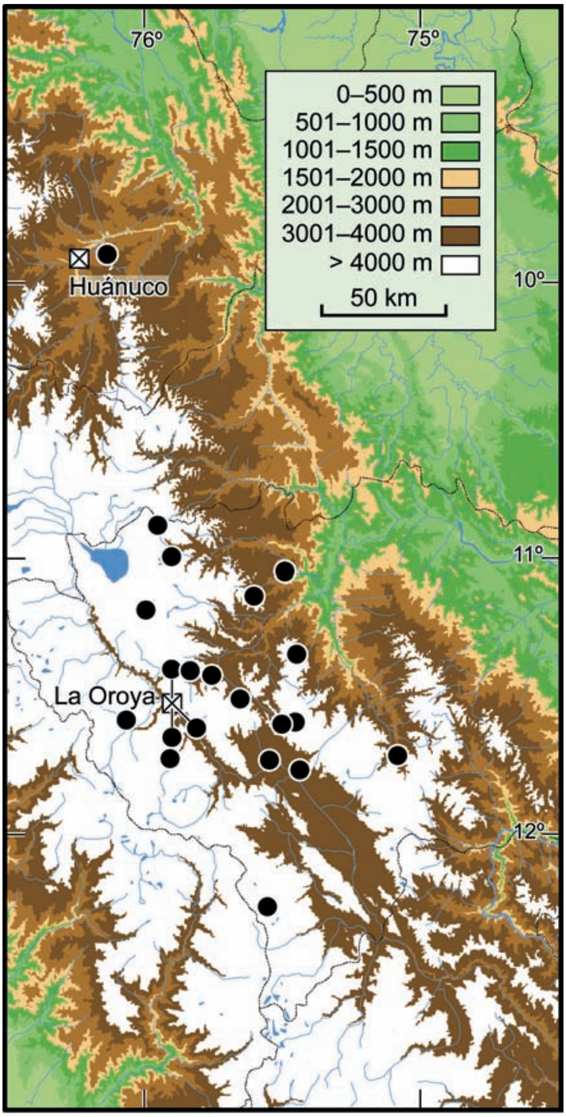

Fig. 12.20 Andean region of central Peru, showing the localities of known occurrences of *Gastrotheca griswoldi*.

Distribution and Ecology

Gastrotheca griswoldi is confined to the high Andes of central Peru (Fig. 12.20). The species occurs at elevations of 3600–4020 m in the upper Río Mantaro Valley on the southern slopes of the Nudo de Pasco, 3650–4060 m on the northern slopes of the Nudo de Pasco, and 3200–3700 m on the eastern slopes of the Andes in the drainages of the Río Perené and Río Huallaga.

The range of *Gastrotheca griswoldi* barely overlaps the extreme southern part of the range of *G. peruana* (vicinity of Paucartambo, Departamento de Pasco). *G. griswoldi* is parapatric with *G. marsupiata* in the upper valley of the Río Mantaro, whereas *G. marsupiata* seems to be restricted to lower elevations.

Individuals are commonly found beneath stones in damp areas by day. In the treeless high Andean region inhabited by these frogs, favorite retreats are in rocky areas in spring seepages and amid piles of stones.

Conservation Status

Gastrotheca griswoldi is categorized as being of Least Concern in the IUCN Red List.

Etymology

The specific name *griswoldi* is a patronym for J. A. Griswold Jr., the collector of the type series.

Remarks

Duellman and Fritts (1972) pointed out that Shreve (1941) was incorrect in assuming that *Gastrotheca griswoldi* was a subspecies of *G. boliviana* [= *marsupiata*]. Vellard (1957) was unaware that the frogs he named *G. bifasciata* were the same as those designated as a subspecies of *G. boliviana* by Shreve.

Duellman and Ruíz-Carranza (1986) noted that the color pattern develops ontogenetically in *Gastrotheca griswoldi*. Of 38 juveniles collected on 20 January 1979 at 32 km S La Oroya, Departamento de Junín, 16 were uniformly green, with snout–vent lengths of 14.8–19.4 mm ($\bar{x} = 17.0$); and 22 were uniformly brown or gray, with snout–vent lengths of 17.5–20.7 mm ($\bar{x} = 19.0$). The green individuals are significantly smaller than the brown ones (ANOVA, $P < 0.005$). Therefore, the authors suggested that by the time juveniles reach an average snout–vent length of 19 mm, the dorsal color changes from a uniform green to brown or gray, and that the pattern develops later.

Gastrotheca (*Gastrotheca*) *lateonota* Duellman and Trueb

Gastrotheca lateonota Duellman and Trueb, 1988:162.—Holotype: KU 181730 from 31.5 km [by road] E Canchaque, 2770 m (5°22′ S, 79°33′ W), Cordillera de Huancabamba, Región de Piura, Peru.

Diagnosis

Adults of this moderately large species attain a snout–vent length of 63.7 mm. The tibia length is more than 50% of the snout–vent length, and is slightly shorter than the foot. The interorbital distance is noticeably greater than the width of the upper eyelid. The skin on the dorsum is smooth or granular, not co-ossified with skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first and second fingers are equal in length; the discs on the fingers are much wider than the digits. The fingers are unwebbed; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is green or brown, with or without darker paravertebral marks. Markings on the head consist of a pale labial stripe and a dark canthal stripe. A pale dorsolateral stripe is present. The flanks are brown, with pale spots; the venter is creamy gray, with brown flecks.

Gastrotheca lateonota most closely resembles *G. monticola* and *G. stictopleura*, both of which differ by having bluntly rounded or sloping snouts in profile, as opposed to a truncate snout in *G. lateonota*, which has a proportionately smaller head than *G. stictopleura*. The three species differ in ventral coloration: dull grayish brown in *G. lateonota*, creamy tan with a few black flecks in *G. stictopleura*, and cream with black spots in *G. monticola*. *G. dysprosita* has a bluntly rounded snout in profile. It also differs from *G. lateonota* by having a green dorsum with a narrow yellow middorsal stripe, and green flanks with small yellow spots; furthermore, *G. dysprosita* lacks a dark canthal stripe and pale labial stripe. In *G. lateonota* and *G. stictopleura*, the frontoparietals do not have otic flanges in contact with median flanges of the squamosals, as they do (forming a temporal arcade) in *G. dysprosita* and *G. monticola*. Individuals of *G. lateonota* that have a green dorsum and distinct pale dorsolateral and supracloacal stripes superficially resemble *G. orophylax* and *G. plumbea*, but in those two latter species the first finger is shorter than the second, as opposed to being of equal length in *G. lateonota*; also, the venter is uniformly pale, as contrasted with the grayish-brown venter in *G. lateonota*.

Description

The following description is based on 18 specimens. The body is robust. The maximum known snout–vent length is 63.7 mm in females; males are unknown. The head is not casqued or co-ossified and is slightly wider than long, as wide as the body. The snout is bluntly rounded in dorsal view, and is truncate in profile; it does not project beyond the anterior margin of the jaw. The canthus rostralis is rounded in cross-section. The loreal region is barely concave; the lips are rounded. The top of the head is slightly depressed. The interorbital distance is about 150% of the width of the upper eyelid. The internarial area is flat. The nostrils are slightly protuberant, and are directed anterolaterally at a point below the terminus of the canthus rostralis and slightly posterior to the anterior margin of the lower lip. The diameter of the eye is slightly less than its distance from the nostril. The tympanum is vertically ovoid, and is separated from the eye by a distance about twice the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately heavy and smooth, extends from the posterior corner of the orbit to a point above the insertion of the arm, and obscures the upper edge of the tympanum.

The arm is moderately slender; ulnar tubercles are absent. The hand is moderate in size. The fingers are moderately long, slender, and unwebbed. The discs on the fingers are large and round; the width of the disc on the third finger is about 30% greater than the length of the tympanum. The relative lengths of the fingers are I = II < IV < III. The subarticular tubercles are moderately small and round; the supernumerary tubercles are small, round, and in a single row on the proximal segments of the fingers. The palmar tubercle is low and bifid; the prepollical tubercle is elliptical; the condition of the nuptial excrescences is unknown. The hind limb is robust. The tibia length is about 48% of the snout–vent length; the foot length is only about 40% of the snout–vent length. Calcars on the heels and tubercles on the tarsi are absent. An outer tarsal fold is absent; the inner tarsal fold is distinct, and is curved throughout the entire length of the tarsus. The inner metatarsal tubercle is elevated, elongately elliptical, and barely visible from above; an outer metatarsal tubercle is absent. The toes are long and slender. The relative lengths of the toes are I < II < III < V < IV. The toes are about one-third webbed; the webbing formula is **I**2—2**II**2—(2½–3)**III**(2^{-}–2)—(3–3½)**IV**(3–3½)—2**V**. The subarticular tubercles are moderately small and round. The supernumerary tubercles are smaller, round, and present only on the proximal segments of the digits.

The skin on the dorsum of the body and limbs is weakly areolate; the skin on the flanks is strongly areolate; the skin on the side of the head is weakly granular; the skin on the throat, chest, belly, and proximal posteroventral surfaces of the thighs is granular; the other surfaces are smooth. There are flat tubercles ventrolateral to the cloacal opening. The opening of the brood pouch is U-shaped, with the anterior border posterior to the level of the sacrum. The dentigerous processes of the vomers are posteromedially inclined, and are narrowly separated medially between the moderately large round choanae. Each process bears six to eight teeth.

COLOR IN PRESERVATIVE

The dorsal surfaces of the head, body, and limbs and the loreal region are bluish gray, brown, or tan. In 77% of the specimens, broad irregular brown or dark bluish-gray paravertebral marks, narrowly bordered by black, extend from the eyelids to a point above the cloacal opening. The dorsal surfaces of the shanks and feet are marked with brown or dark bluish-gray spots (not distinct transverse bars), narrowly outlined with black: four or five spots on each shank, and three or four on each tarsus. The dorsal surfaces of the thighs and forearms are either uniformly colored or marked with small black spots. A narrow creamy tan dorsolateral stripe begins on the canthus and extends to the groin. A pale cream labial stripe begins below the eye and extends to the insertion of the arm. The tympanic region and flanks are dark brown; the groin and anterior and posterior surfaces of the thighs are bluish gray, with small black flecks. In 45% of the specimens, a pale supracloacal stripe and a dark patch in the cloacal region are present. The throat is dark grayish brown; the chest and belly are dull creamy gray, with brown flecks.

COLOR IN LIFE

The dorsum is bright green, green with brown paravertebral markings, tan with brown paravertebral markings, or dark brown (Fig. 12.21). The dorsolateral stripe is bronze cream. The flanks are brown, mottled with green or tan; the axilla, groin, anterior and posterior surfaces of the thighs, and hidden surfaces of the shanks and feet are blue, with black flecks. The toes and fingers are bronze tan, with or without black flecks. The belly is grayish tan, with gray or brown flecks. The iris is deep bronze, with fine black reticulations (W. E. Duellman field notes, 27 February 1979).

MEASUREMENTS

Males and female are about the same size, but there are significant differences in some measurements (Table 12.10).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous semicoarse pattern of shallow pits and low rounded ridges. The nasals articulate medially, and are fused to one another and the sphenethmoid posteriorly; posterolaterally, the nasal lacks an articulation with the anterolateral margin of the frontoparietals. The frontoparietals have a complete articulation medially, a narrow supraorbital flange, and a moderate otic flange. A temporal arcade is absent. The frontoparietal covers only the anterior epiotic eminence; the carotid canal is partially closed, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for about half the

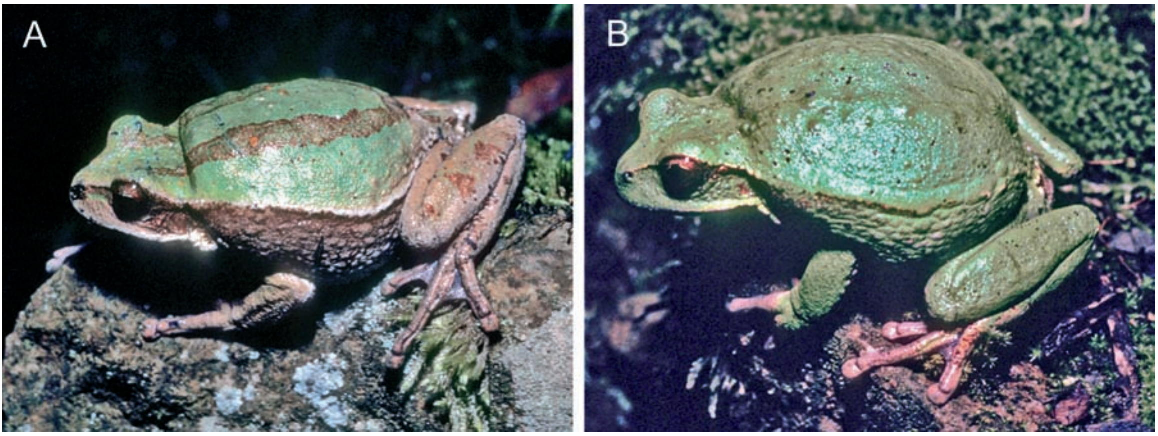

Fig. 12.21 *Gastrotheca lateonota.* A: KU 181730 (holotype), female, 62.1 mm SVL. B: KU 181732, female, 54.6 mm SVL. Both from El Tambo, Piura, Peru. Photos by W. E. Duellman.

Table 12.10 Univariate statistics for adults of *Gastrotheca lateonota*

	Males ($n = 4$)			Females ($n = 14$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	58.8	54.8–61.4	0.82	59.2	54.0–63.7	3.32
Tibia length	25.5	23.7–26.3	1.19	27.2	23.2–30.2	2.02
Foot length**	23.1	14.8–27.3	5.81	28.7	24.6–31.8	2.24
Head length	18.1	17.3–19.2	0.78	18.4	16.4–20.0	1.12
Head width	20.0	19.0–20.6	0.72	20.5	17.4–22.2	1.35
Interorbital distance	6.4	5.7–7.0	0.56	6.2	5.5–6.9	0.44
Eyelid width	4.8	4.4–5.2	0.35	4.4	3.9–5.1	0.40
Internarial distance	3.8	3.7–3.9	0.11	3.7	3.1–4.2	0.33
Eye diameter*	5.0	4.8–5.6	0.38	5.4	5–5.8	0.20
Eye–nostril distance	4.8	4.4–5.2	0.44	4.8	4.4–5.2	0.30
Orbit–jaw distance	2.9	2.4–3.1	0.32	2.8	2.4–3.3	0.22
Nostril–jaw distance	3.9	3.8–4.1	0.14	4.0	3.5–4.6	0.32
Tympanum diameter**	3.8	3.5–4.0	0.24	2.9	2.4–3.8	0.45
Thumb length*	9.9	9.4–10.7	0.59	10.9	9.5–12.7	0.82
Third finger length	18.6	16.9–19.9	1.34	20.0	17.5–21.8	1.42
Disc width**	2.6	2.4–2.9	0.21	3.0	2.7–3.5	0.26

*Differences between the means of the sexes are significant (ANOVA, $P \leq 0.05$).

**Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The maxilla has a low but distinct postorbital process, which articulates with the wide zygomatic ramus of the squamosal. The head of the squamosal has a narrow crest; the narrow otic plate articulates marginally with the crista parotica. The dorsal part of the stapedial footplate is about three times the size of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified posterior to the midlength of the orbit, but is not synostosed with the prootic. The neopalatines are widely separated medially, and bear a low irregular ridge ventrally. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a long acuminate recurved process on the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located between the anterior quadrants of the choanae.

Life History

At El Tambo, Peru, 13 brooding females were moving into a depression filling with water during a heavy rain on the night of 27 February 1979. These females contained 64–152 hatching eggs ($\bar{x} = 110$) in Stages 31–35. Thus this species produces free-living aquatic tadpoles.

Advertisement Call

No calls have been associated with this species.

Distribution and Ecology

This species is known from the type locality, at an elevation of 2770 m in cloud forest on the Pacific slopes of the Cordillera de Huancabamba in northern Peru, as well as at an elevation of 3163 m in the Cordillera Occidental in Provincia de El Oro in southwestern Ecuador (Fig. 12.22).

Conservation Status

This species is categorized as Data Deficient in the IUCN Red List.

Etymology

The specific name was derived from the Latin adjective *lateo*, meaning "hidden," and the Latin noun *nota*, meaning "character"; the name was used in reference to the cranial characters that, although hidden by the skin, readily distinguish this species from *Gastrotheca monticola* (Duellman and Trueb, 1988).

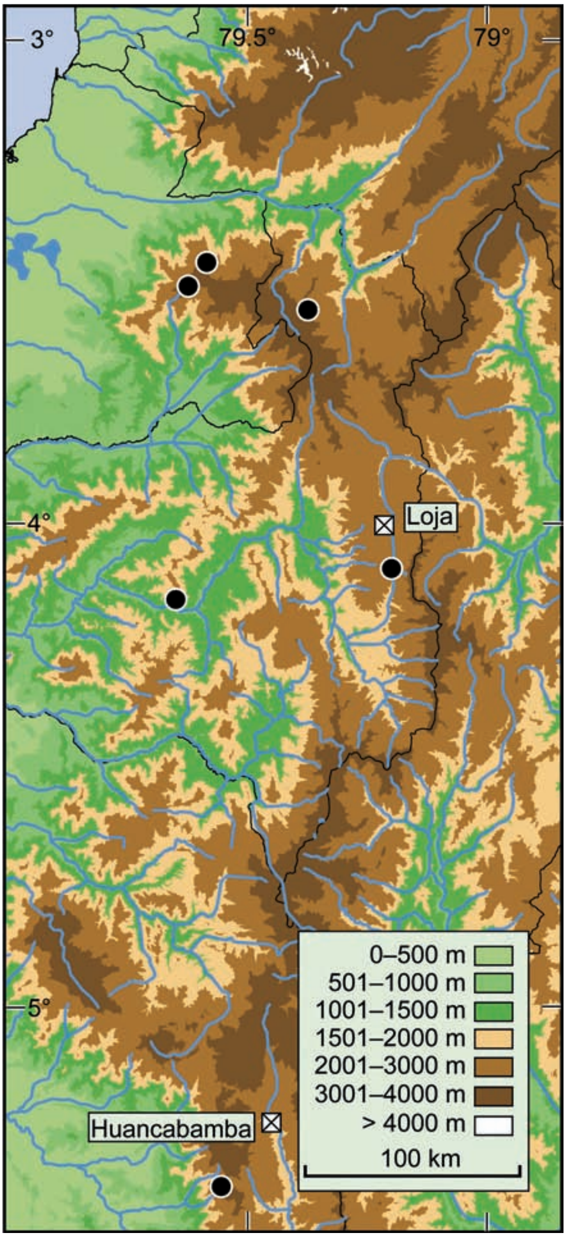

Fig. 12.22 Andean region of southern Ecuador and northern Peru, showing the localities of known occurrences of *Gastrotheca lateonota.*

Remarks

Gastrotheca lateonota was distinguished from *G. monticola* by osteological characters (Duellman and Trueb, 1988) and immunological differences (Duellman et al., 1988). In the phylogenetic analysis of molecular data, it is the sister taxon to *G. pseustes*.

Gastrotheca (*Gastrotheca*) *marsupiata* (Duméril and Bibron)

Hyla marsupiata Duméril and Bibron, 1841:598.—Holotype: MNHN 4877 from Cusco, Región de "Cuzco" [= Cusco], Peru.

Nototrema marsupiatum—Günther, 1859:116.

Chorophilus cuzcanus Cope, 1877:37.—Holotype: from "Peru" [now lost]. Synonymy fide Duellman and Fritts, 1972:17.

Leptodactylus (*Plectromantis*) *andicola* Boettger, 1891:346.—Types: "Umgebung von Sorata, Bolivia" [now lost, fide Heyer, 1978:33]. Synonymy fide Lynch and McDiarmid, 1987:340.

Nototrema bolivianum Steindachner, 1892:840.—Lectotype (designated by Duellman and Fritts, 1972:4): NMW 16490 from Puerto de San Mateo, Departamento de Cochabamba, Bolivia. Synonymy fide Duellman and Fritts, 1972:17.

Eleutherodactylus binghami Stejneger, 1913:542.—Holotype: USNM 49559 from Cusco, Región de Cusco, Peru. Synonymy fide Duellman and Fritts, 1972:17.

Eleutherodactylus footei Stejneger, 1913:543.—Holotype: USNM 49562 from Tincochalca, Región de Cusco, Peru. Synonymy fide Duellman and Fritts, 1972:17.

Gastrotheca boliviana—Barbour and Noble, 1920:611.

Gastrotheca bifasciata vellardi Laurent, 1969a:129 [substitute name for *Gastrotheca marsupiata marsupiata* sensu Vellard, 1957].

Gastrotheca marsupiata—Duellman and Fritts, 1972:17.

Gastrotheca (*Gastrotheca*) *marsupiata*—Dubois, 1987:32.

Diagnosis

Adults of this moderately small species attain a maximum snout–vent length of 49.6 mm. The tibia length is less than 50% of the snout–vent length, and is slightly shorter than the foot. The interorbital distance is slightly greater than the width of the upper eyelid. The skin on the dorsum is weakly granular to weakly pustular, not co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is shorter than the second; the discs on the fingers are slightly wider than the digits. The fingers are unwebbed; on the foot the webbing extends maximally to the antepenultimate subarticular tubercles on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is gray, green, or tan with darker spots, usually arranged in paravertebral rows. Markings on the head consist of a dark canthal stripe and (usually) a pale labial stripe and dark interocular bar. A pale dorsolateral stripe is absent. The flanks are pale, with dark spots or mottling; the venter is creamy white, with or without dark flecks.

Gastrotheca marsupiata can be distinguished from other high-Andean and southern Andean species of *Gastrotheca* (except *G. caeruleomaculata*, *christiani*, and *gracilis*) by the presence of a dark interorbital bar or a T-shaped mark that is not connected to the markings on the back. The interorbital bar, if present, usually is connected to the markings on the dorsum in *G. chrysosticta*, *excubitor*, and *griswoldi*. Of those species that have an interorbital bar connected to the dorsal markings, the latter consists of a pair of irregular longitudinal marks in *G. christiani*, and three longitudinal marks in *G. gracilis*. *G. piperata* usually lacks an interorbital bar and has a dorsal color pattern consisting of small black flecks, thus differing from *G. marsupiata*, in which the dorsal pattern consists of an interorbital bar and dark spots, usually in paravertebral rows. For a detailed comparison between *G. marsupiata* and *G. piperata*, see the account of the latter species. *G. caeruleomaculata* differs from *G. marsupiata* by having blue spots on the dorsum and flanks.

Description

The following description is based on 180 specimens. The body is robust; the maximum snout–vent length is 41.6 mm in males, and 49.6 mm in females. The head is slightly wider than long, but not as wide as the body. The snout is acutely rounded in dorsal view, and is more bluntly rounded in profile. The canthus rostralis is rounded in cross-section. The loreal region is barely concave; the lips are rounded. The top of the head is flat. The interorbital distance is only slightly greater than the width of the upper eyelid. The internarial area is flat. The nostrils are not protuberant, and are directed anterolaterally at the terminus of the canthus rostralis at a point posterior to the anterior margin of the lower lip. The diameter of the eye is equal to or slightly greater than its distance from the nostril. The tympanum is round, and is separated from the eye by a distance about equal to the length of the tympanum. The tympanic annulus is distinct and smooth; the supratympanic fold is moderately heavy, and extends from the posterior corner of the orbit to a point above the insertion of the arm.

The arm is moderately robust, and bears one row of small low ulnar tubercles. The hand is small. The fingers are moderately long, and bear small round discs; the width of the disc on the third finger is slightly less than the length of the tympanum. The relative lengths of the fingers are I < II < IV < III. The fingers are unwebbed. The subarticular tubercles are small and round; none are bifid. The supernumerary tubercles are minute, subconical, and numerous on the proximal segments. The palmar tubercle is trifid; the prepollical tubercle is elliptical, and bears a nuptial excrescence in breeding males. The hind limb is robust. The tibia length is about 46% of the snout–vent length; the foot length is about 46.5% of the snout–vent length (about 46.5%). The heel lacks a calcar or tubercle. Tarsal tubercles are absent; a weak straight inner tarsal fold is present on the distal half of the tarsus. The inner metatarsal tubercle is low, flat, ovoid, and not visible from above; an outer metatarsal tubercle is absent. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. The toes are webbed basally; the webbing formula is **I**2—2**II**2—3**III**(3–3^-)—(3–4)**IV**(3–4)—(2–3)**V**. The subarticular tubercles are small and subconical; the supernumerary tubercles are minute, subconical, and present only on the proximal segments.

The skin on the dorsum is smooth (0.6%), granular (70.5%), or pustular (28.9%); the skin on the flanks and ventral surfaces of the throat, chest, belly, and thighs is granular. Cloacal folds and tubercles are absent. The opening of the brood pouch is narrowly U-shaped, with the anterior margin at the level of the posterior edge of the sacrum. The dentigerous processes of the vomers are slightly inclined posteromedially, and are narrowly separated medially between the small ovoid choanae. Each process bears three to six teeth.

COLOR IN PRESERVATIVE

The dorsum is dull tan to gray, usually (97%) with darker markings consisting solely of flecks (2%) or dark spots (95%). Pale spots are present in 97% of the specimens, including all of those with dark spots. A dark interorbital bar usually (97%) is present; a dark canthal stripe and a pale labial stripe usually (93%) are present. A pale dorsolateral stripe and a supracloacal stripe are absent. The flanks are uniformly pale (7%) or have irregular dark spots or mottling (93%). The anterior surfaces of the thighs are uniformly pale (10%), or have either dark mottling (57%) or spots or vertical bars (33%). The posterior surfaces of the thighs are uniformly pale (51%) or have dark spots (49%). The dorsal surfaces of the limbs are uniformly pale (10%) or have dark transverse bars (90%). The chest and belly are uniformly pale (66%) or have dark flecks (34%); the ventral surfaces of the limbs are uniformly pale; the vocal sac is dull gray.

COLOR IN LIFE

In all of the large series of specimens seen in life, some individuals are brown and others are green; most indi-

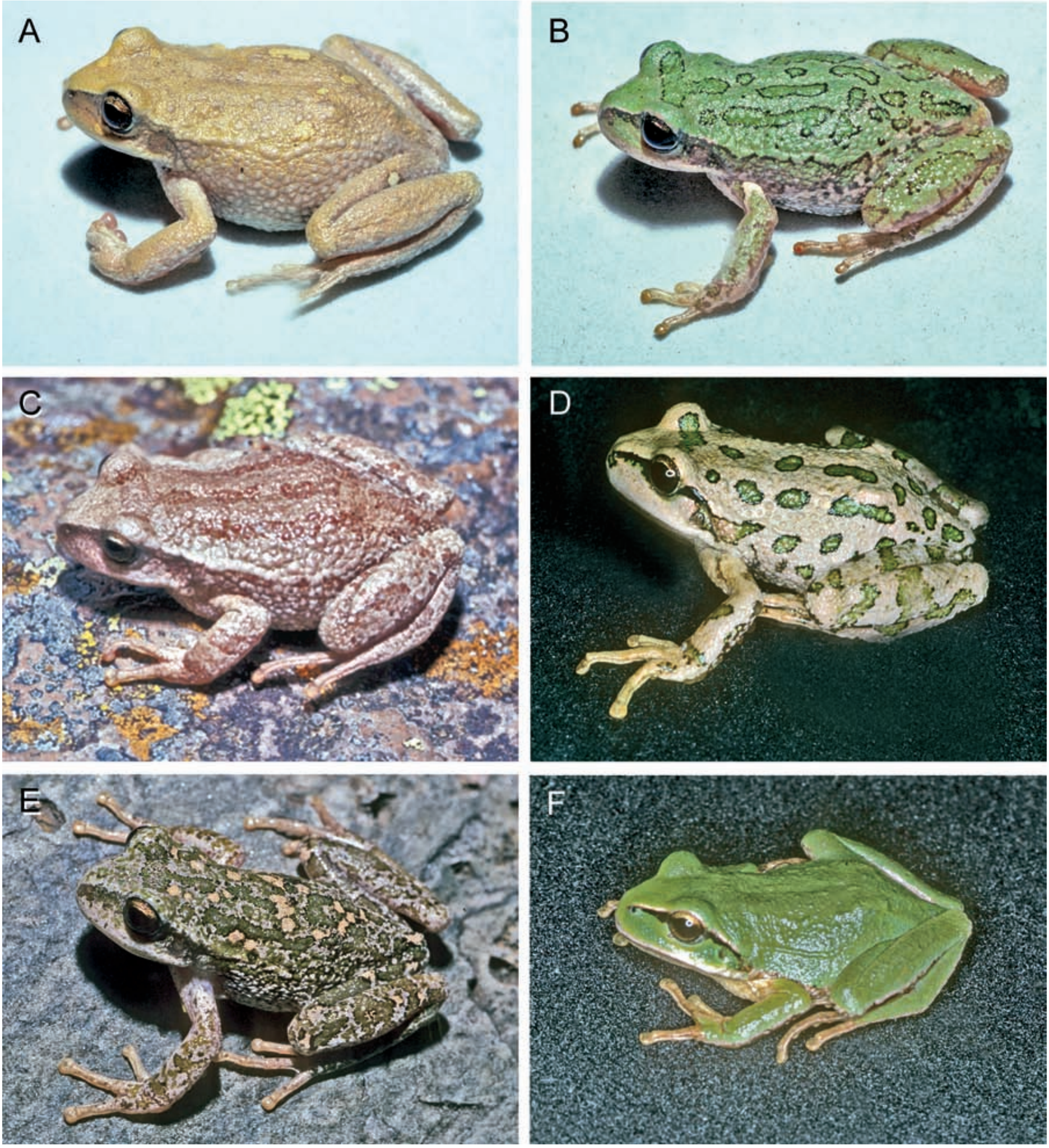

Fig. 12.23 Variations in the colors and patterns in *Gastrotheca marsupiata*. A: KU 163219, female, 36.6 mm SVL, Abra Socclaccossa, 3900 m, Apurimac, Peru. B: KU 163220, male, 31.7 mm SVL, same locality. C: KU 163232, male, 32.4 mm SVL, Abra Soraccocha, 3720 m, Apurimac, Peru. D: KU 139185, male, 33.3 mm SVL, Tambomachay, 3650 m, Cusco, Peru. E: KU 163189, female, 35.6 mm SVL, Abra Huancarane, 3790 m, Cusco, Peru. F: KU 139447, juvenile, 24.0 mm SVL, Chilca, 2760 m, Cusco, Peru. Photos by W. E. Duellman.

viduals have darker brown or green markings on the dorsum; and most individuals have small pale spots on the dorsum (Fig. 12.23). The iris is metallic bronze. Variation in life is documented by the following descriptions of specimens from diverse localities in Peru.

Two adults (KU 138243–44) from Pampas, Región de Huancavélica.—The dorsum is yellowish beige, with olive-green markings having gold-beige centers. The canthus rostralis and postorbital area are olive green, with a gold line extending from the nostril, below the eye, to the tympanum. The upper lip is beige. The anterior and dorsal surfaces of the thighs are beige, with greenish-brown bars; the posterior surfaces of the thighs are beige, with white flecks. The venter is grayish white (T. H. Fritts field notes, 23 October 1969).

Eleven adults and one juvenile (KU 138297–306, 138399–400) from Huancavélica, Región de Huancavélica.—The adults either have a uniformly brown dorsum (1 specimen), a yellowish-tan dorsum with pale yellow spots (1), or a pale brown to grayish-brown dorsum with olive-green to leaf-green markings (9); most of latter have a few yellow spots. The one juvenile is golden brown, with olive markings. The posterior and ventral surfaces of the thighs are pale brown to grayish brown, with white flecks; the dorsal and anterior surfaces of the thighs are pinkish beige, with medium brown to moss-green markings (T. H. Fritts field notes, 15 October 1969).

Fourteen adults (KU 163232–45) from 35 km W Andahuaylas, Región de Apurímac.—All have a tan to brown dorsum; most individuals have dark brown markings, but some have green markings. Most individuals also have cream flecks on the dorsum. The posterior surfaces of the thighs are grayish tan; the venter is dirty cream (W. E. Duellman field notes, 16 February 1975).

Seven adults and one juvenile (KU 138252–59) from 10 km E Abra Huillque, Región de Cusco.—The dorsum is grayish beige to bronze beige; all adults except one female have numerous yellow spots on the dorsum. One male lacks dorsal dark markings; one male has faint algal-green dorsal markings; one male has bronze dorsal markings; the remaining males and females have leaf-green dorsal markings. The one juvenile is uniformly yellow green. The posterior surfaces of the thighs are beige to grayish brown, with beige flecks and white tubercles (T. H. Fritts field notes, 24 November 1969).

Two adults (KU 138319–20) from Granja de la Raya, Región de Cusco.—In one adult the dorsum is pale gray, with yellow-green markings mostly outlined by black. The dorsal and lateral surfaces of the head are yellowish green, with beige canthal and postorbital stripes bordered below by black stripes. There is a beige labial stripe. The posterior surfaces of the thighs are pale green, with white tubercles. The second individual has a grayish-brown dorsum, with darker yellowish-green markings and pale yellow spots. The head and loreal region are pale brown, with a green suffusion; the canthal and labial stripes are grayish beige. The dorsal surfaces of the thighs are gray, with yellowish-green bars; the posterior surfaces of the thighs are pale green, with white tubercles (T. H. Fritts field notes, 12 December 1969).

Twenty-three individuals (KU 139155–77) from San Jerónimo, Región de Cusco.—Most were pale bronze tan when collected; later some changed to brown, and a few were green. The dorsal markings were dark green or brown; all adults and some juveniles had small yellow spots on the dorsum. The posterior surfaces of the thighs were pinkish to rosy brown, with cream tubercles proximally. The axilla and groin were bluish gray in adults; this color was especially noticeable in large females (W. E. Duellman field notes, 6 January 1971).

Twenty-seven specimens (KU 163160–86) from 4 km W Santa Rosa, Región de Puno.—The dorsum is tan, with dark green markings; some individuals have creamy yellow spots. The posterior surfaces of the thighs are pinkish tan; the venter is creamy white (W. E. Duellman field notes, 3 February 1975).

MEASUREMENTS

Although females are larger than males, and the means of four of their measurements are significantly different from those of males, the variances of most measurements in both sexes are non-homogeneous (Table 12.11). The variance in males tends to be leptokurtotic, whereas that in females is platykurtotic. This skewness in measurements is evident in both the pooled sample from several localities and the sample from the vicinity of Cusco.

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a heterogeneous pattern; the sphenethmoid bears vermiform or ramus ridging; the rest of the skull table has a semicoarse pattern of shallow pits and low rounded ridges. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially, but lack a distinct supraorbital flange and an otic flange. A temporal arcade is absent. The frontoparietal does not cover the epiotic eminences; the carotid canal is open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are scarcely deflected posteriorly, at an angle less than 10°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for three-fourths the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with

Table 12.11 Univariate statistics for adults of *Gastrotheca marsupiata*

	Males (n = 88)			Females (n = 85)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length**	35.0	30.6–41.6	2.20†	37.7	30.9–49.6	4.08
Tibia length	15.9	13.6–18.4	1.09†	17.4	12.8–23.6	2.38
Foot length	16.1	13.3–19.0	1.18†	17.9	14.1–25.1	2.34
Head length	11.2	9.1–13.0	0.80†	11.5	9.2–15.0	1.23
Head width	12.3	10.7–14.1	0.78†	12.9	10.6–16.6	1.25
Interorbital distance	3.2	2.3–3.8	0.28†	3.5	2.4–5.1	0.40
Eyelid width	2.9	2.2–3.5	0.29†	3.1	2.2–4.3	0.40
Internarial distance	2.2	1.3–2.9	0.40†	2.5	1.5–3.1	0.32
Eye diameter**	3.3	2.4–4.6	0.38	3.4	2.6–4.3	0.37
Eye–nostril distance**	3.0	2.1–3.7	0.33	3.2	2.5–4.3	0.38
Orbit–jaw distance**	1.3	0.6–2.1	0.31	1.5	0.7–2.3	0.29
Nostril–jaw distance	2.2	1.7–3.1	0.31	2.3	1.8–3.1	0.33
Tympanum diameter	1.7	1.1–2.3	0.25	1.8	1.4–2.6	0.26
Thumb length	5.8	4.6–8.0	0.68†	6.2	4.6–8.5	0.82
Third finger length	10.4	8.7–12.2	0.69†	11.5	9.2–15.1	1.31
Disc width	1.5	1.1–1.8	0.17†	1.6	1.2–2.4	0.24

**Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

†Variances are non-homogeneous (Levene's test for equal variances, $P < 0.05$), but those for the Brown-Forsythe test are significant ($P < 0.05$).

the dental process of the premaxilla. The quadratojugal is short. The maxilla lacks a distinct postorbital process, but articulates with the slender zygomatic ramus of the squamosal. The head of the squamosal has a narrow crest; the narrow otic plate articulates marginally with the crista parotica. The dorsal part of the stapedial footplate is about three times the size of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has an acuminate terminus anterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are narrowly separated medially, and bear a low irregular ridge ventrally. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a long acuminate recurved process on the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located between the middle quadrants of the choanae.

Life History

The eggs hatch as tadpoles, which complete their development in shallow ponds. Twelve brooding females collected in October, December, and January from Región de Cusco, Peru, have snout–vent lengths of 33.7–43.3 mm ($\bar{x}$ = 39.2). They were brooding 63–167 eggs ($\bar{x}$ = 101.2) having diameters of 2.9–4.0 mm ($\bar{x}$ = 3.3). A brooding female collected on 15 October gave birth to tadpoles on 6 December, so the duration of brooding lasts at least 52 days. These tadpoles were maintained in the laboratory at a temperature of 20°C–22°C for 42 days, at which time they died. A developmental series through Stage 39 was preserved (Table 12.12).

Tadpoles

A typical tadpole in Stage 39 (KU 204031) has a body length of 19 mm, and a total length of 45 mm. In dorsal view the body is elliptical; the sides are nearly parallel along half the length of the body. In dorsal view the snout is bluntly rounded; in profile it is highest posteriorly, and is not as high as wide. The snout is inclined from the nostrils to the bluntly rounded tip. The throat is barely concave. The eyes are moderately small, and are directed dorsolaterally. The interorbital distance is about one-third the width of the body at the level of the orbits. The nostrils are about midway between the eyes and the tip of the snout. The spiracular tube is short and sinistral; the spiracular opening is directed posterodorsally on the ventrolateral surface at about midlength of the body. The cloacal tube is short and dextral, with a diagonal opening. The caudal musculature is moderately robust, and is higher than the dorsal fin at midlength of the tail; the musculature terminates in a pointed tip well within the margin of the caudal fin. The dorsal fin arises gradually from the proximal part of the caudal musculature. The dorsal and ventral

Table 12.12 Growth and developmental stage for tadpoles of *Gastrotheca marsupiata*. Measurements are in mm for a single tadpole, except for day 42, which is the average of 10 individuals.

Age (days)	Stage	Body Length	Total Length
Birth	30	4.4	10.0
1	31	5.7	13.5
3	31	6.2	14.2
6	32	8.4	19.2
8	33	8.7	22.3
11	34	8.9	23.4
14	34	11.6	29.1
16	34	11.8	29.4
18	35	14.0	33.4
20	35	14.4	35.9
22	35	15.2	36.1
24	35	15.4	37.0
26	35	15.5	36.5
28	36	16.8	42.0
30	36	16.7	42.3
34	36	16.8	42.9
36	37	18.4	47.5
38	38	19.8	50.0
40	39	19.2	51.7
42	39	20.5	45.6

fins are subequal in height at midlength of the tail; the fins terminate in a bluntly rounded tip.

The width of the oral disc is about one-third the width of the body; the disc is bordered laterally and ventrally by a single row of short blunt marginal papillae. There are two upper and three lower rows of labial teeth; the upper rows are longest and are equal in length; the lower rows are progressively shorter; the second upper row is narrowly interrupted medially. The upper jaw sheath is massive, with each side of the sheath forming a sigmoid arch on the cutting surface; the lower jaw sheath also is massive, and is broadly V-shaped; both sheaths bear a few short blunt serrations.

In life the dorsum of the body is olive green to grayish green, with or without faint metallic-green flecks; the venter is darker gray green, with a pinkish tint. The caudal musculature is greenish gray to tan; the caudal fins are translucent, with or without yellowish-green flecks. In individuals with well-developed hind limbs, a dark gray interorbital bar, narrow golden canthal line, and dark gray postorbital mark are evident. The iris is bronze.

Advertisement Call

Vocalization by *Gastrotheca marsupiata* was studied by Sinsch (1988) and Sinsch and Joermann (1989), who recognized different kinds of calls: a territorial call (termed an advertisement call by Sinsch and Joermann, 1989), consisting of a single note; an aggressive call, consisting of a long note followed by two to seven (usually three) short notes; and a breeding call, consisting of a short note repeated every 1–10 seconds.

Distribution and Ecology

Gastrotheca marsupiata occurs from the Nudo de Pasco in central Peru to southern Bolivia (Fig. 12.24). The species is known from elevations of 2760–4360 m in the drainages of Río Mantaro, Río Apurimac, and Río Urubamba in Peru; the Lago Titicaca Basin in southern Peru and Bolivia; the Altiplano of Bolivia; and the eastern slopes of the Andes of Bolivia, from Departamento de La Paz to Departamento de Chuquisaca. The species descends in some of the valleys in the eastern slopes of the Andes; for example, it occurs as low as 2760 m at Chilca in the valley of the Río Urubamba, Peru, and as low as 2500 m at Cochabamba, Bolivia.

Gastrotheca marsupiata occurs syntopically with *G. excubitor* at Abra Acjanaco, Región de Cusco, Peru. At other high ridges along the eastern front of the Andes in Región de Cusco (e.g., Abra Amparaes and Abra Málaga), *G. excubitor* inhabits higher elevations than *G. marsupiata* and descends the windward and wetter Amazonian slopes, whereas *G. marsupiata* seems to be restricted to the drier leeward slopes below the crests. At Abra Tapuna, Región de Ayacucho, *G. marsupiata* occurs syntopically with *G. pacchamama*. Both *G. excubitor* and *G. pacchamama* have direct development. The range of *G. marsupiata* is parapatric with that of another direct-developing species (*G. griswoldi*) in the upper valley of the Río Mantaro in Región de Junín, Peru. There, *G. griswoldi* occurs at elevations of more than 3600 m, whereas *G. marsupiata* is at elevations below 3600 m.

Most of the localities at which *Gastrotheca marsupiata* occurs are bleak, treeless, and windswept; the natural vegetation consists almost exclusively of bunchgrasses of the genus *Stipa*. By day the frogs can be found beneath stones or beneath bunchgrass overhanging the edges of narrow irrigation or drainage ditches. At night males have been found calling from irrigation ditches and from seepage areas amid bunchgrass. This species tolerates low temperatures: calling males have been found at temperatures of 0°C when snow was falling, and by day frogs have been found beneath stones covered with snow. Tadpoles seem to develop in whatever water is available: sites range from small stagnant puddles to shallow grassy ponds, irrigation ditches, and small streams.

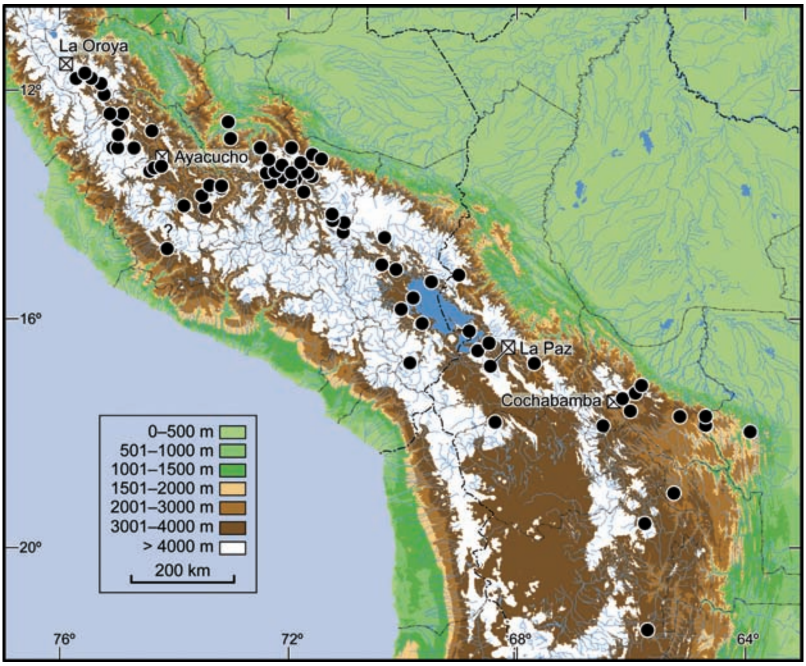

Fig. 12.24 Andean region of central and southern Peru and Bolivia, showing the localities of known occurrences of *Gastrotheca marsupiata*.

Table 12.13 Numbers of specimens of *Gastrotheca marsupiata* from different localities used in the analyses. The morphometric analyses are based only on adults; the analyses of structural characters and coloration are based on all specimens.

Population	Males	Females	Subadults	Total
Junín	—	—	1	1
Huancavélica	9	14	2	25
Apurimac	10	21	13	44
Cusco	64	43	—	107
Bolivia	6	6	1	13

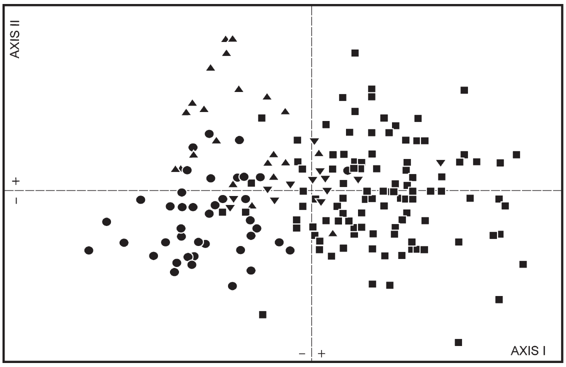

Fig. 12.25 Multivariate plot of a stepwise discriminant analysis of morphometrics of *Gastrotheca marsupiata* from four areas in the Andes. Circles = Apurimac, Peru (*n* = 37); squares = Cusco, Peru (*n* = 102); triangles = Huancayo, Peru (*n* = 23); inverted triangles = Bolivia (*n* = 13).

Conservation Status

According to the ICUN Red List, *Gastrotheca marsupiata* is categorized as being of Least Concern. Aguilar et al. (2012) noted that the species may be endangered in areas of mineral concessions in Ayacucho, Peru.

Etymology

The specific name *marsupiata* refers to the dorsal pouch, or marsupium.

Remarks

Geographic variation was analyzed using five samples, ranging from central Peru to Bolivia (Table 12.13). Morphometric data were analyzed using a stepwise discriminant functions analysis (Fig. 12.25). In a jackknifed six-step model of $\log_{10}$ data, only 74% of the specimens were classified correctly according to population. Of the populations from northwest of Río Apurimac (Departamentos de Apurimac and Huancavélica), only three specimens fall within the range of the populations from southeast of Río Apurimac, and only six of the latter fall within the range of the northern populations. In Figure 12.25, the variables that entered the model on the first axis indicate that the head is larger in most of the specimens from Huancavélica than in those from Apurimac, whereas the variation in head size in the sample from Cusco is as great as that in the two northern populations. The second axis is primarily an overall size factor; specimens from Apurimac and Huancavélica have smaller snout–vent lengths than do those from Cusco and Bolivia. Separate cluster analyses of structural characters and coloration revealed no geographic patterns in the variations. Thus, although the low arid valley of the Río Apurimac may be a barrier to gene flow at the present time, on the basis of morphological characters it is not possible to separate samples from either side of the valley. There seems to be only a general trend in overall size.

Subsequent to the completion of the foregoing analysis, I had the opportunity to examine additional specimens from various localities in Bolivia. All of these specimens are like the southern Peruvian *G. marsupiata* in size and structure, but they display considerable variation in coloration.

CET specimens from Tablasmontes, Departamento de Cochabamba.—Twenty individuals have a dorsal pattern of three continuous or fragmented dorsal marks: a median mark extending from the interorbital region (in 7 specimens) or the occiput (13) to the sacral region, and paravertebral marks extending from the eyelid (3) or temporal region (17) to the sacral region. A pale dorsolateral stripe is present in 7 individuals. The side of the head and flanks are brown (17), or the flanks are tan with brown spots (3). A pale labial stripe is present, at least posteriorly. The anterior and posterior surfaces of the thighs are uniformly tan. A pale supracloacal stripe is absent; a dark patch in the cloacal region is present in 9 individuals. One specimen has a dark interorbital mark that is connected to the median longitudinal mark. The venter is creamy tan, with dark flecks on the throat (all 20) and also on the chest (5); the other 15 have extensive dark mottling or spots on the chest and belly. Ten males with brown nuptial excrescences have snout–vent lengths of 25.9–34.4 mm ($\bar{x} = 31.3$), and 32.5–40.2 mm ($\bar{x} = 36.8$) in eight adult females.

ZMFK 55247–48 (males) 55246 (female) from Arque, Departamento de Cochabamba.—Two adult males with snout–vent lengths of 27.7 and 30.5 mm, and a female with a snout–vent length of 35.5 mm, have irregular dark spots and round white spots on the dorsum.

A gravid female from Remate, Departamento de Cochabamba.—This specimen has a snout–vent length of 42.3 mm and scattered dark flecks on the dorsum.

CET specimen from between Corani and Colomi, Departamento de Cochabamba.—A single subadult has a broad interorbital mark, three irregular rows of dark spots and scattered small white spots on the dorsum, spotted flanks, and a uniformly cream venter.

As is evident from the synonymy, the highly variable color pattern has resulted in a plethora of specific names applied to this species. For more than a hundred years after the description of *G. marsupiata* from Peru, herpetologists erroneously applied that name to frogs from Ecuador, as specimens from that area were better represented in European museums. Steindachner (1892) recognized that Ecuadorian and Bolivian specimens were different, and he described the latter as *Nototrema bolivianum*. The type locality of *N. bolivianum* was given by Steindachner (1892:5) as "Bolivia, Provinz Yuracares bei Puerto de S. Mateo am oberen Chaparé." The name Puerto de San Mateo is no longer used, but the region is in the tropical forested Andean foothills at an elevation of 500–1000 m, and thus is outside the elevational and ecological range of *G. marsupiata*. In external features, coloration, and osteology (determined from radiographs), the lectotype of *N. bolivianum* (NMW 16490), designated by Duellman and Fritts (1972), is like *G. marsupiata* from the Bolivian highlands, and thus was placed in the synonymy of *G. marsupiata* by these authors. As noted by Duellman and Köhler (2005), Puerto de San Mateo was near an old road, which in the late 1800s was one of the few passageways between the Bolivian highlands and the lowlands. Conceivably, the type series of *N. bolivianum* came from the higher elevations, and the stated type locality could be an error.

Vellard (1957) confused Shreve's (1941) description of *Gastrotheca boliviana griswoldi* with *G. marsupiata* and thus named that taxon *G. marsupiata bifasciata* [= *G. griswoldi*]. Vellard's (1957) application of names to populations in central and southern Peru was influenced by his having little topotypic material available of *G. marsupiata*, a species about which he obviously was confused. Nonetheless, Vellard did recognize that the Ecuadorian populations were different from those in southern Peru; accordingly, he proposed the name *G. marsupiata ecuatoriensis* for the Ecuadorian populations. Laurent (1969a), in turn, misinterpreted Vellard's (1957) allocation of *G. marsupiata*. Laurent (1969a) considered *G. marsupiata bifasciata* to be a species distinct from *G. marsupiata*, and he proposed the name *G. bifasciata vellardi* for the populations in southern Peru that were recognized as *G. marsupiata marsupiata* by Vellard (1957). Duellman and Fritts (1972) assigned *G. boliviana* to the synonymy of *G. marsupiata*, and *G. bifasciata* to the synonymy of *G. griswoldi*, and they showed that the name *Hyla riobambae* Fowler, 1913, was available for the Ecuadorian species.

If future studies reveal that the frogs in Bolivia now referred to the taxon *Gastrotheca marsupiata* are distinct from *G. marsupiata*, as potentially is shown by limited molecular data, Steindachner's (1892) name *Nototrema bolivianum* may have priority. Yet this name is preceded by *Leptodactylus* (*Plectromantis*) *andicola* Boettger, 1891, which was placed in the synonymy of *G. marsupiata* by Lynch and McDiarmid (1987). I strongly suspect that the marsupial frogs living on the Altiplano of Bolivia will be shown to be conspecific with those in the Titicaca Basin in southern Peru.

Other names (*Chorophilus cuzcanus*, *Eleutherodactylus binghami*, *Eleutherodactylus footei*) in the synonymy of *G. marsupiata* are based on juveniles. The justification for placing these names in the synonymy of *G. marsupiata* was provided by Duellman and Fritts (1972).

All of the papers published on the reproduction of "*Gastrotheca marsupiata*" in which the source of their material is given refer to *G. riobambae* (see the discussion of "Life History" in the account of that species).

Gastrotheca (*Gastrotheca*) *nebulanastes* Duellman, Catenazzi, and Blackburn

Gastrotheca nebulanastes Duellman, Catenazzi, and Blackburn, 2011:3.—Holotype: KU 173210 from Buenos Aires, on Paucartambo–Pilcopata road, 2280 m, 13°09′16″ S, 71°35′11″ W, Distrito de Kosñipata, Provincia de Paucartambo, Región de Cusco, Peru.

Diagnosis

Adults of this moderately small species attain a maximum snout–vent length of 40.7 mm. The tibia length is 49%–56% of the snout–vent length, and is slightly longer than the foot. The interorbital distance is about 1.5 times the width of upper eyelid. The skin on the dorsum is moderately tubercular, not co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is longer than the second; the discs on the fingers are notably wider than the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing is basal between the third, fourth, and fifth toes; the other toes are unwebbed. The dorsum is brown or green, with darker brown markings. Markings on the head consist of a dark brown interorbital bar. A pale dorsolateral stripe is absent. The flanks are tan, with black spots; the venter is dull creamy tan.

Gastrotheca nebulanastes is parapatric with *G. excubitor* and *G. marsupiata*, which occur at higher elevations. The tibia length is less than 50% of the snout–vent length in *G. excubitor*, and usually more than 50% in *G. nebulanastes*. The length of the tibia is less than the length of the foot in *G. excubitor*, but greater than the length of the foot in *G. nebulanastes*. In *G. excubitor* the snout is bluntly rounded in profile, whereas it is truncate in *G. nebulanastes*, which also has a coarsely granular dorsum, compared with the smooth dorsum in *G. excubitor*. Other structural differences include the relative lengths of the first and second fingers (first equal to or shorter than the second in *G. excubitor*, and longer than the second in *G. nebulanastes*). An inner tarsal fold is weak on the distal half of the tarsus in *G. excubitor*, and absent in *G. nebulanastes*. The toes are about one-third webbed in *G. excubitor*, in contrast to only basal webbing in *G. nebulanastes*. The two species also differ in coloration. A dark canthal stripe and pale labial stripe are present in *G. excubitor* but absent in *G. nebulanastes*, which also has dark brown vertical bars on the anterior surfaces of the thighs, in contrast to these surfaces being uniformly tan or tan with brown mottling in *G. excubitor*. *G. marsupiata*, which differs from all of the species considered here in the diagnosis by having eggs that hatch as tadpoles instead of direct development into froglets, also differs from *G. nebulanastes* in several structural features: a more acutely rounded snout in dorsal view; smooth skin on the dorsum, with low rounded granules (coarsely granular in *G. nebulanastes*); first finger shorter than the second (longer than the second in *G. nebulanastes*); tibia length less than 50% of the snout–vent length and shorter than the foot (usually more than 50% and longer than the foot in *G. nebulanastes*); and a distinct tarsal fold on the distal half of the tarsus (fold absent *G. nebulanastes*). The dorsum is pale tan to pale green, with irregular brown or green markings, as well as a dark canthal stripe and pale labial stripe in *G. marsupiata*, whereas the dorsum is much darker and canthal and labial stripes are absent in *G. nebulanastes*.

Gastrotheca antoniiochoai is essentially sympatric with *G. nebulanastes*, and differs from the latter by having the skin on the dorsum weakly shagreen (coarsely granular in *G. nebulanastes*), a dark canthal stripe (absent in *G. nebulanastes*), first finger shorter than the second (longer than the second in *G. nebulanastes*), and an interorbital distance less than the width of the upper eyelid (much greater than the width of the upper eyelid in *G. nebulanastes*). *G. excubitor* has a single median brood pouch, whereas *G. antoniiochoai* has paired lateral brood pouches, a feature otherwise known only in *G. zeugocystis* in Región de Huánuco in the Andes in central Peru. *G. nebulanastes* might be confused with *G. ochoai*, a slightly smaller species, which is like *G. nebulanastes* in having the interorbital space being much greater than the width of the upper eyelid and discs on the fingers much wider than the adjacent digit, but *G. ochoai* differs from *G. nebulanastes* by having an acuminate snout in dorsal view (bluntly rounded in *G. nebulanastes*), smooth to finely granular skin on the dorsum (coarsely granular in *G. nebulanastes*), and the first finger shorter than the second (longer than the second in *G. nebulanastes*). The only other small species of *Gastrotheca* on the humid slopes of the Andes in central and southern Peru are *G. atympana* from Región de Junín, *G. pachachacae* from Región de Apurímac, and *G. rebeccae* from Región de Ayacucho. *G. atympana* is unique in the genus by lacking a tympanum. *G. pachachacae* differs from *G. nebulanastes* in lacking a dark interorbital bar (present in *G. nebulanastes*) and in having a narrower interorbital area, shorter tibia, first finger slightly longer than the second, and discs on the fingers that are slightly wider than the digits proximal to the discs (much wider than the digits in *G. nebulanastes*). *G. rebeccae* is like *G. nebulanastes* in having a broad interorbital area, discs on the fingers that are much wider than the digits proximal to the disc, and a tibia longer than the foot, but it differs from *G. nebulanastes* by having the first finger shorter than the second (longer than the second in *G. nebulanastes*), snout acutely rounded in dorsal view and bluntly rounded in profile (bluntly rounded in dorsal view and truncate in profile in *G. nebulanastes*), smooth to weakly granular skin on the dorsum (coarsely granular in *G. nebulanastes*), and a dark canthal stripe and pale labial stripe (stripes absent in *G. nebulanastes*).

Description

The following description is based on 23 specimens. The body is robust; the maximum known snout–vent lengths are 38.3 mm in males, and 40.7 mm in females. The head is slightly wider than long. The snout is rounded in dorsal view, and is nearly truncate in profile; it extends slightly beyond the margin of the lower lip. The canthus rostralis is round in cross-section. The loreal region is slightly concave; the lips are round. The top of the head is flat. The interorbital distance is about 1.5 times the width of the upper eyelid. The internarial area is flat. The nostrils are barely protuberant, directed laterally at the terminus of the canthus rostralis at a point slightly posterior to the level of the anterior margin of the lower jaw. The diameter of the eye is about equal to its distance from the nostril. The tympanum is round, and is separated from the eye by a distance half again the length of the tympanum. The tympanic annulus is distinct and smooth. A weak supratympanic fold extends from the posterior corner of orbit to a point posterodorsal to the tympanum.

The arm is slender; ulnar tubercles are absent. The hand is moderately large. The fingers are long and unwebbed. The discs on the fingers are moderately large and rounded; the width of the disc on the third finger is equal to the length of the tympanum. The relative lengths of the fingers are I > II < IV < III. The subarticular tubercles are prominent and round; none are bifid. The supernumerary tubercles are minute, subconical, and numerous on the proximal segments of the fingers. The palmar tubercle is low, flat, and ovoid; the prepollical tubercle is elliptical. The hind limb is robust. The tibia length usually is more than 50% of the snout–vent length, and is slightly longer than the foot. Calcars, tarsal tubercles, and inner tarsal folds are absent. The outer metatarsal tubercle is minute and round; the inner metatarsal tubercle is large, elliptical, and barely visible from above. The toes are long. The relative lengths of the toes are I < II < III < V < IV. The toes are not webbed, except for basal webbing between the fourth and fifth toes in all specimens, and also between the third and fourth toes in six individuals. The subarticular tubercles are small and round; the supernumerary tubercles are minute, round, and numerous on the proximal segments of the toes.

The skin on the dorsum is granular, with two to five large white granules ventral or posteroventral to the tympanum; the skin on the flanks is areolate; the skin on the throat, belly, and ventral surfaces of the thighs is granular; the other surfaces are smooth. Cloacal tubercles and folds are absent. The pouch opening is broadly V-shaped, with the anterior border at the level of the posterior edge of sacrum. The vomerine odontophores are inclined posteromedially, and are narrowly separated medially between the round choanae. Each process bears three to five teeth.

COLOR IN PRESERVATIVE

The dorsum is brown, with darker brown markings consisting of an interorbital bar usually connected to either a middorsal or roughly bifurcate mark that extends to the sacral region or beyond. The flanks are tan, with dark brown to black markings, which are either prominent spots or vertical bars. Three dark brown transverse bars on the dorsal surfaces of the thighs are continuous with a dark brown longitudinal mark on the posterior surface of the thigh. There are three diagonal dark brown bars on each shank, and three or four such bars on each foot. A faint creamy white supracloacal stripe and short heel stripes are discernable in most specimens. Except for the dark brown interorbital bar, head markings (if present) are indistinct.

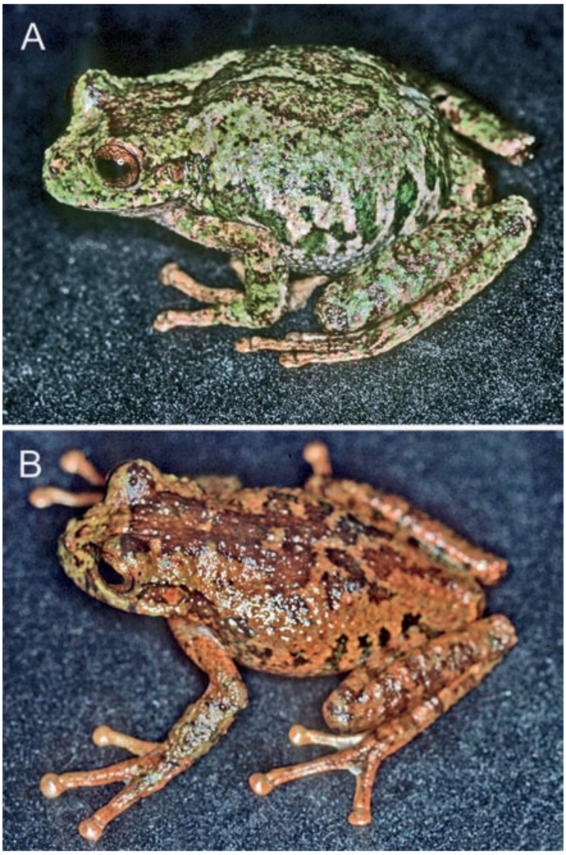

Fig. 12.26 *Gastrotheca nebulanastes.* A: KU 173208, female, 40.7 mm SVL. B: KU 173209, male, 36.0 mm SVL. Both from Buenos Aires, Cusco, Peru. Photos by W. E. Duellman.

COLOR IN LIFE

The dorsum is dull green, with dark brown to black markings; the flanks are colored like the dorsum, except with an orange-brown suffusion; the hidden surfaces of the limbs are orange brown; the venter is metallic tan. The tympanum is brown; a single small white spot is present on the left side of the dorsum. The iris is pale bronze tan, with black reticulations (Fig. 12.26).

KU 173208–18, a series from the type locality.—The dorsum is pale grayish tan, yellowish tan, or olive tan, with dark brown or metallic-green markings. Cream spots are present on some individuals. The flanks, groin, and anterior and posterior surfaces of the thighs are creamy tan to reddish brown, with blue, bluish-green, or dark brown spots. The webbing is tan; the fingers and toes are tan. The venter is metallic bronze brown. There are metallic creamy bronze tubercles along the posterior upper jaw. The iris is pale bronze, with fine black reticulations (W. E. Duellman field notes, 19 January 1977).

MEASUREMENTS

Males are slightly smaller than females, but the proportions of the two sexes do not seem to be different (Table 12.14).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous coarse pattern of shallow pits and low rounded ridges. The nasals neither articulate medially with one another nor posterolaterally with the frontoparietals; their borders are distinct from the sphenethmoid. The frontoparietals lack a complete articulation medially, and have a narrow supraorbital flange and a small otic flange. A temporal arcade is absent. The frontoparietal does not cover the epiotic eminences; the carotid canal is partially closed, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for about three-fourths the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The maxilla lacks a distinct postorbital process; the slender zygomatic ramus of the squamosal articulates with the margin of the pars facialis of the maxilla. The head of the squamosal has a narrow crest; the narrow otic plate articulates marginally with the crista parotica. The dorsal part of the stapedial footplate is two to three times the size of the ventral part, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are widely separated medially, and are smooth ventrally. The pterygoid articulates with the medial surface of the pars facialis of the maxilla via a broad low process on the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located between the middle quadrants of the choanae.

Life History

Throughout most of the year, males call from grasses, shrubs, trees, terrestrial and arboreal bromeliads, and from the ground in the montane scrub or understory of cloud forest. The eggs hatch into froglets. One female

Table 12.14 Univariate statistics for adults of *Gastrotheca nebulanastes* from the type locality

	Males ($n = 18$)			Females ($n = 4$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	35.4	32.3–38.3	1.74	37.7	35.8–40.7	1.81
Tibia length	18.3	17.0–19.7	0.68	20.3	19.4–21.4	0.73
Foot length	16.6	13.8–18.5	1.02	18.1	17.5–18.8	0.51
Head length	12.9	11.4–12.7	0.37	13.5	12.2–16.4	1.68
Head width	12.9	12.4–13.5	0.48	14.0	12.5–14.9	0.95
Interorbital distance	4.7	3.9–5.4	0.47	4.7	4.4–5.0	0.26
Eyelid width	3.1	2.9–3.2	0.08	3.2	3.1–3.3	0.08
Internarial distance	2.4	1.5–2.9	0.48	1.8	1.4–2.2	0.29
Eye diameter	3.4	2.7–3.8	0.24	3.6	3.5–3.8	0.14
Eye–nostril distance	3.1	2.8–3.3	0.13	3.3	3.1–3.6	0.19
Orbit–jaw distance	1.4	1.1–1.6	0.20	1.2	1.1–1.3	0.09
Nostril–jaw distance	2.7	2.0–3.0	0.30	2.6	2.5–2.8	0.14
Tympanum diameter	1.8	1.4–2.1	0.25	1.8	1.6–2.1	0.22
Thumb length	6.6	5.6–7.2	0.49	6.9	6.6–7.3	0.26
Third finger length	11.5	10.3–11.9	0.47	12.6	12.0–13.3	0.48
Disc width	1.7	1.4–2.1	0.17	2.1	2.0–2.3	0.16

(MUSM 20940) having a snout–vent length of 35.8 mm contains eight oviducal eggs. Another female (KU 173208) collected on 19 January gave birth to 17 young on 25–27 January. Most young emerged from the pouch surrounded by external gills (Fig. 7.17). Kicking by the young breaks through the gill membrane. Essentially the entire froglet is outside of the pouch before the gills are ruptured. Two young had broken gill stalks before emerging from the pouch. Froglets in the anterior part of the pouch were removed by the female inserting one or both feet (plantar surface up) into the pouch, making digging motions, and stretching the pouch opening. This action was employed for 8–10 minutes for each of two young and one undeveloped egg.

The newly born froglets had snout–vent lengths of 9.5–9.8 mm ($\bar{x} = 9.64 \pm 0.21$). At birth the dorsum was creamy tan, with a grayish-brown interorbital bar and dorsolateral mark. Two days after birth the dorsum was brown, with dark brown markings; the throat was white; the belly was transparent; the rest of the venter was yellow.

Advertisement Call

Duellman et al. (2011) described the advertisement call as consisting of a long note 689–916 milliseconds ($\bar{x} = 818.2 \pm 70.0$) in duration, with 37–47 pulses ($\bar{x} = 41.6 \pm 3.2$), and one or more secondary notes. Secondary notes have a duration of 24–54 milliseconds ($\bar{x} = 30.9 \pm 7.8$), emphasized frequencies of 1653–1730 Hz (median = 1692), and typically are single pulsed. The pulse rate in long notes is 49.5–53.7 Hz ($\bar{x} = 51.0 \pm 1.2$) at temperatures of 10.7°C–12.3°C. Long notes have some frequency modulation: fundamental frequencies with a maximum energy range of 1461–1615 Hz (median = 1500 Hz) for the third pulse, 1538–1884 Hz (median = 1634 Hz) for a central pulse, and 1653–1769 Hz (median 1730 = Hz) for the third-to-last pulse. Pulses emitted at the highest amplitude in long notes have frequencies of 1653–1962 Hz (median = 1730 Hz) and are generally located in the second half of the note (after the twentieth pulse), although amplitude modulation varies among calls and does not always increase constantly during the long note.

Distribution and Ecology

Gastrotheca nebulanastes is known from elevations of 2000–3300 m in the upper Río Kosñipata Valley on the northeastern slope of Abra Acjanaco in the Cordillera Oriental in Región de Cusco in southern Peru (Fig. 12.27). All of these localities are in the Parque Nacional Manu, where the frogs occur in cloud forest along the road between Paucartambo and Pilcopata. This area contains cloud forest on steep slopes with tree ferns, moss-covered cliffs, and cascading streams. The species also is know from an elevation of 2770 m in the Río Marcapata Valley, about 70 km ESE of the Kosñipata Valley.

Elevational records in the Kosñipata Valley for juvenile and adult specimens captured in the field ($n = 33$) indicate that this species is most abundant between 2600 and 2800 m, where it inhabits the montane scrub: ridges of steep slopes covered with Andean alder, shrubs, and

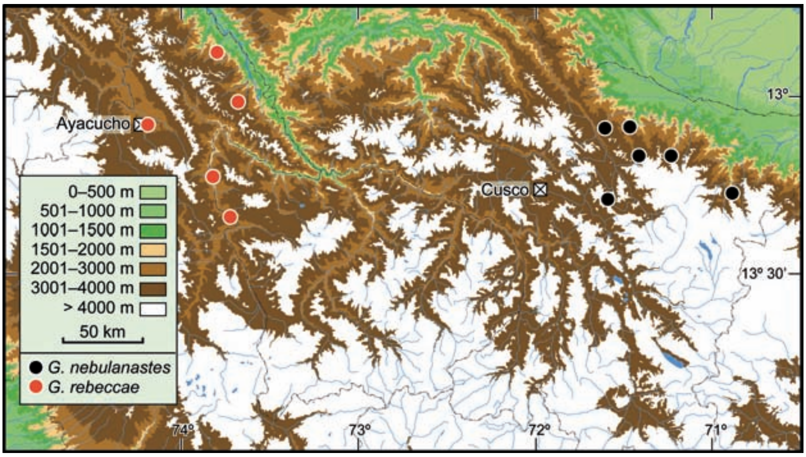

Fig. 12.27 Andean region of southern Peru, showing the localities of known occurrences of *Gastrotheca nebulanastes* and *G. rebeccae*.

an abundance of terrestrial mosses, lycophites, and lichens. There is sharp transition from cloud forest to the puna characteristic of the Abra Ajcanaco that is inhabited by *Gastrotheca excubitor* and *G. marsupiata*.

Conservation Status

One of the two known geographic populations of *Gastrotheca nebulanastes* exists in the Parque Nacional Manu, one of the largest protected areas in South America. Therefore it may be protected from habitat destruction, but the chytrid fungus *Batrachochytrium dendrobatidis* has been reported in one individual of *G. nebulanastes* from the upper Kosñipata Valley (Catenazzi et al., 2011). This frog has not been categorized by the IUCN, but its status probably should be listed as Vulnerable.

Etymology

According to Duellman et al. (2011), the specific name is derived from the Latin *nebula*, meaning “fog,” and the Greek *nastes*, meaning “dweller.” The name was applied because the upper Kosñipata Valley inhabited by this species commonly is enshrouded in fog.

Remarks

In the upper Río Kosñipata Valley, 18 other adults were captured and 16 were measured in the field. The snout–vent lengths were 36.3 and 40.9 mm in two females, and 27.8–35.8 mm in males ($\bar{x} = 32.4 \pm 2.2$, $n = 14$). Two females weighed 4.8 and 5.0 g, and 14 males weighed 1.6–3.9 g ($\bar{x} = 2.4 \pm 0.6$).

Some differences in color patterns are evident in preserved specimens from the Río Marcapata Valley, compared with those in the Río Kosñipata Valley. In those from the former locality, pale supracloacal stripes and heel stripes are absent in all specimens, whereas these stripes are present in all individuals from the Río Kosñipata Valley. Likewise, the venter is flecked in all specimens from the Río Kosñipata Valley, but flecks are present in only 71% of the 14 specimens from the Río Marcapata Valley.

Gastrotheca (*Gastrotheca*) *ochoai* Duellman and Fritts

Gastrotheca ochoai Duellman and Fritts, 1972:27.—Holotype: KU 139202 from SW base of Cordillera de Vilcanota, 2760 m, W Río Runtumayo, about 3 km N Chilca, 10 km [by road] NW Ollantaytambo, Región de Cusco, Peru.

Gastrotheca (*Opisthodelphys*) *ochoai*—Dubois, 1987:31.

Diagnosis

This moderately small species attains a maximum snout–vent length of 37.5 mm. The tibia length is less than <55% of the snout–vent length, and is slightly longer than the foot. The interorbital distance is noticeably greater than the width of the upper eyelid. The skin on the dorsum is smooth to finely granular with scattered tubercles, not co-ossified with skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is shorter than the second; the discs on the fingers are much wider than the digits. The fingers are unwebbed; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is tan, with small dark spots and/or flecks. Markings are absent on the head. A pale dorsolateral stripe is absent. The flanks are tan, with dark spots; the venter is creamy gray.

Gastrotheca ochoai differs from all other southern Andean *Gastrotheca* (except *G. christiani*, *chrysosticta*, and *gracilis*) by having tuberculate skin on the dorsum. The tubercles are small and scattered in *G. ochoai*, whereas they are large and scattered in *G. chrysosticta*, and moderately large and uniformly distributed in the other species. Furthermore, *G. christiani* and *G. chrysosticta*, as well as *G. excubitor* and *G. marsupiata* (which are sympatric with *G. ochoai*), have a dorsal pattern usually consisting of a dark interorbital bar and dark paravertebral markings; these plus a middorsal mark are present in *G. gracilis*. The dorsum in *G. ochoai* is brown, with dark flecks or small spots; a narrow middorsal dark mark is present in about one-third of the specimens, all of which lack a dark interorbital bar. *G. piperata* has black flecks on the dorsum and small tubercles on the head and upper eyelids, but it differs from *G. ochoai* by having proportionately much smaller discs on the fingers, an interorbital distance about equal to the width of the upper eyelid, a pale labial stripe, and a dark canthal stripe. *G. pachachacae* also lacks markings on the head, but it differs from *G. ochoai* by having a rounded snout in dorsal view, a much narrower interorbital distance, and a small calcar on the heel.

Description

The following description is based on 42 specimens. The body is moderately slender; the maximum snout–vent length is 30.4 mm in males, and 37.5 mm in females. The head is wider than long, but not as wide as the body. The snout is acuminate in dorsal view, and is bluntly rounded in profile. The canthus rostralis is angular in cross-section. The loreal region is concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 150% of the width of the upper eyelid. The internarial area is flat. The nostrils are not protuberant, and are directed laterally at the terminus of the canthus rostralis at the level of the anterior margin of the lower jaw. The diameter of the eye is slightly less than its distance from the nostril. The tympanum is vertically ovoid, and is separated from the eye by a distance slightly greater than the length of the tympanum. The tympanic annulus is distinct and smooth; the supratympanic fold is weak, and extends from the posterior corner of the orbit to a point above the insertion of the arm.

The arm is moderately robust, and lacks ulnar tubercles. The hand is small. The fingers are moderately long, and bear moderately large elliptical discs; the width of the disc on the third finger is 1.5 times the length of the tympanum. The relative lengths of the fingers are I < II < IV < III. The fingers are unwebbed. The subarticular tubercles are small and round; the supernumerary tubercles are minute, round, and present only on the proximal segments. The palmar tubercle is low, flat, and bifid; the prepollical tubercle is elliptical, and bears a nuptial excrescence in breeding males. The hind limb is moderately robust. The tibia length is about 50% of the snout–vent length; the foot length is about 45% of the snout–vent length. A calcar, tarsal tubercles, and tarsal folds are absent. The outer metatarsal tubercle is minute and subconical; the inner metatarsal tubercle is small, elliptical, and not visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. The inner toes are not webbed; the outer toes are webbed basally; the webbing formula is **III**3½—3**IV**3—2**V**. The subarticular tubercles are small and round; the supernumerary tubercles are minute, and are present only proximally.

The skin on the dorsum is smooth (64%) or granular (36%) with scattered small tubercles; the skin on the flanks, belly, and ventral surfaces of the thighs is granular. Cloacal tubercles and folds are absent. The opening of the brood pouch is U-shaped, with the anterior margin at the level of the posterior edge of the sacrum. The dentigerous processes of the vomers are posteromedially inclined, and are narrowly separated medially between the posterior margins of the ovoid choanae. Each process bears three or four teeth.

COLOR IN PRESERVATIVE

The dorsum is dull tan to pale gray, with dark brown to black flecks or spots. A diffuse middorsal dark mark is present in 31% of the specimens. The flanks are uniformly pale tan (17%) or have dark spots (83%). The anterior and posterior surfaces of the thighs are uniformly dark brown. The chest and belly are uniformly pale creamy gray (65%) or have small dark spots (35%). The throat is pale gray. Dorsolateral, labial, canthal, and supracloacal stripes are absent.

COLOR IN LIFE

The dorsum is pale tan to bronze, with brown markings (Fig. 12.28). The iris is metallic bronze, with fine black reticulations. Variation in coloration is evident from the following descriptions of living individuals.

Fourteen individuals (KU 138649–62) from Chilca, Región de Cusco, Peru.—The dorsum is golden beige to golden brown, with black to brown flecks; the flecks in some individuals are interconnected to form one large indistinct chevron. The canthus rostralis is dark brown, grading to golden yellow in the loreal region. The dark brown of the canthus extends through the eye and onto the anterior half of the body, where in some specimens it takes on a greenish cast. The anterior and posterior surfaces of the thighs are yellow

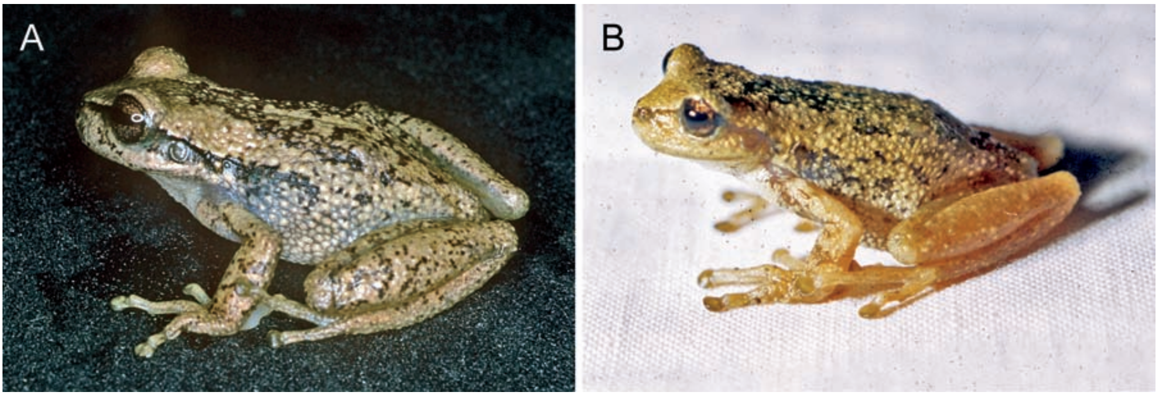

Fig. 12.28 *Gastrotheca ochoai*. A: KU 139203, male, 29.5 mm SVL, Chilca, 2760 m, Cusco, Peru. B: KU 138666, female, 39.3 mm SVL, Ollachea, 2800 m, Puno, Peru. Photos by W. E. Duellman (A) and T. H. Fritts (B), KUDA.

Table 12.15 Univariate statistics for adults of *Gastrotheca ochoai*. Differences between the means of the sexes for all measurements are significant (ANOVA, $P \leq 0.01$).

	Males (n = 17)			Females (n = 15)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	29.2	28.2–30.4	0.63†	34.7	31.2–37.5	2.08
Tibia length	14.8	14.2–15.6	0.43†	18.0	16.1–19.3	0.92
Foot length	13.1	11.7–14.4	0.82†	15.8	12.4–18.8	1.83
Head length	9.3	8.7–10.1	0.36†	10.8	9.9–11.6	0.57
Head width	9.8	9.3–10.6	0.43†	11.8	10.8–12.9	0.82
Interorbital distance	3.4	3.0–3.8	0.19†	4.1	3.6–5.0	0.42
Eyelid width	2.5	1.9–2.8	0.20	2.7	2.4–3.3	0.28
Internarial distance	1.7	1.4–2.6	0.26	1.9	1.6–2.6	0.22
Eye diameter	2.6	2.3–2.9	0.19	2.9	2.5–3.8	0.30
Eye–nostril distance	2.9	2.5–3.3	0.20	3.4	3.1–3.8	0.20
Orbit–jaw distance	1.3	0.8–1.6	0.21	1.5	1.2–2.0	0.25
Nostril–jaw distance	2.2	1.9–2.5	0.18	2.5	2.0–2.7	0.19
Tympanum diameter	1.4	1.1–1.9	0.20	1.6	1.5–1.9	0.15
Thumb length	5.0	4.1–5.5	0.40†	5.7	4.5–6.9	0.73
Third finger length	8.8	7.6–9.6	0.57†	10.5	9.1–12.2	0.98
Disc width	1.4	1.0–1.8	0.22	1.8	1.5–2.2	0.24

†Variances are non-homogeneous (Brown-Forsythe test, $P \leq 0.05$).

beige, with a few yellow spots near the cloaca. The dorsal surfaces of the thighs are golden beige, with distinct black flecks; the forearm is bronze beige to yellow beige (T. H. Fritts field notes, 17 January 1970).

A large series (KU 138666–718) from Ollachea, Región de Puno, Peru.—The dorsum is yellow, with a slight yellowish-bronze tint and irregular dark brown blotches on the dorsum. Males and subadult females have a rust-red tint on the head. The canthus rostralis is greenish brown; the loreal region is bronze. The tympanum and an irregularly defined dark brown to greenish-brown stripe extend from the eye to the flank. The thighs are yellowish tan, with yellow spots dorsally; the venter is white, with a bluish tint posteriorly in females (T. H. Fritts field notes, 24 January 1970).

MEASUREMENTS

Females are larger than males; the differences between the means of all measurements are significant (Table 12.15).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the rest of the skull table, is smooth and lacks dermal sculpturing. The nasals neither articulate medially with one another nor posterolaterally with the frontoparietals; their borders

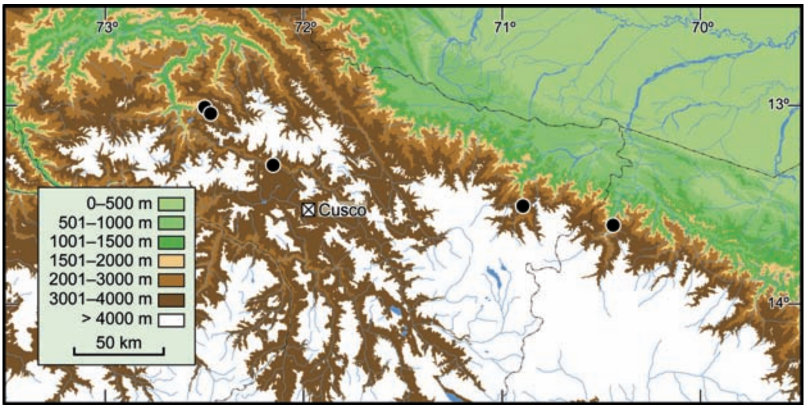

Fig. 12.29 Andean region of southern Peru, showing the localities of known occurrences of *Gastrotheca ochoai*.

are distinct from the sphenethmoid. The frontoparietals lack a complete articulation medially, as well as supraorbital and otic flanges. A temporal arcade is absent. The frontoparietal does not cover the epiotic eminences; the carotid canal is partially closed, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process of the pars facialis of the maxilla is visible; the maxilla articulates with the dorsally adjacent nasal for less than one-fourth the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is long. The maxilla lacks a distinct postorbital process; the slender zygomatic ramus of the squamosal does not articulate with the margin of the pars facialis of the maxilla. The head of the squamosal lacks a crest; the narrow otic plate articulates marginally with the crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal size, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has an acuminate terminus anterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are moderately separated medially, and bear a low irregular ridge ventrally. The pterygoid lacks an expansion of the anterior ramus of the bone and, therefore, any articulation with the maxilla or the squamosal. The vomers bear minute dentigerous processes located between the posterior quadrants of the choanae.

Life History

The eggs undergo direct development in the pouch. One female collected on 15 November 1969 contained 10 young that were hatching. Four of these young have snout–vent lengths of 13.5–14.5 mm ($\bar{x} = 13.7$). In life they were dull gray, with a black canthus rostralis. Twelve females collected in January 1970, having snout–vent lengths of 31.7–37.5 mm ($\bar{x} = 34.9$), contained 20–22 ovarian eggs ($\bar{x} = 20.7$) having diameters of 3.2–3.4 mm ($\bar{x} = 3.4$).

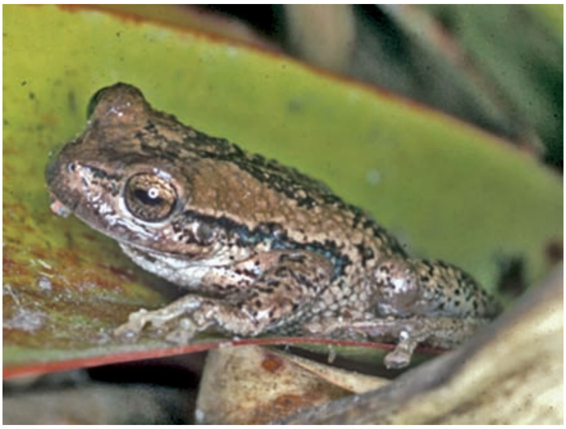

Fig. 12.30 *Gastrotheca ochoai*, one of a series (KU 139203–7), female, in bromeliad, Chilca, 2760 m, Cusco, Peru. Photo by W. E. Duellman.

Advertisement Call

No recordings are available.

Distribution and Ecology

Gastrotheca ochoai is known only from five deep valleys in the eastern face of the Andes in southern Peru (Fig. 12.29), where individuals have been found at elevations of 2745–3080 m. All specimens have been found in small bromeliads growing on cliffs (Fig. 12.30).

Conservation Status

This species is categorized as Data Deficient in the IUCN Red List.

Etymology

The specific name *ochoai* is a patronym for Oscar Ochoa M. of the Universidad Nacional San Antonio Abad del Cusco. For several years he facilitated field work in southern Peru and aided in the collection of the type series of this species.

Remarks

As noted in the description of living individuals, specimens from Chilca are slightly different from those from Ollachea. These are the only two samples for which colors in life and sufficient specimens for statistical analyses are available. The means of three measurements (foot length, thumb length, and third finger length) are significantly larger in both sexes from Ollachea than for specimens from Chilca, whereas the same is true for four measurements (head length, head width, eye diameter, and eye–nostril distance) in males only, and three (interorbital distance, tympanum diameter, and disc width) in females only.

Presumably the populations of *Gastrotheca ochoai* are isolated in the valleys on the eastern front of the Andes; probably they have been separated since a warm interglacial period allowed contact across intervening ridges that now are uninhabitable by the species.

Gastrotheca (*Gastrotheca*) *ossilaginis* Duellman and Venegas

Gastrotheca ossilaginis Duellman and Venegas, 2005: 196.—Holotype: MUSM 19486 from Lago Quindecocha, Juanjui, 3100 m, Provincia de Huallaga, Region de San Martín, Peru.

Diagnosis

This medium-sized species of *Gastrotheca* attains a maximum known snout–vent length of 53.3 mm. The tibia length is about 50% of the snout–vent length, and is slightly shorter than the foot. The interorbital distance is about twice the width of the eyelid. The skin on the dorsum is finely shagreen, co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar, but bears low tubercles. The tympanic annulus is smooth. The first finger is shorter than the second; the discs on the fingers are slightly wider than the digits proximal to the discs. The fingers are unwebbed; the toes are about one-fourth webbed. The dorsum is green or tan. Usually there are no markings on the head. A pale dorsolateral stripe is absent. The flanks are colored like the dorsum; the venter is creamy gray.

The skin is co-ossified with the underlying cranial elements in 12 other species of *Gastrotheca*. Of these, four species (*G. fissipes*, *megacephala*, *prasina*, and *recava*) have broad casqued heads with extensive co-ossification; four others (*G. galeata*, *nicefori*, *ovifera*, and *weinlandii*) differ from *G. ossilaginis* by having a bony transverse occipital ridge, which has four dorsal projections in *G. ovifera*. *G. galeata* differs from all of the others and from *G. ossilaginis* by having the premaxillae and maxillae flared, to create a spatulate skull. *G. antomia*, *bufona*, and *guentheri* differ from *G. ossilaginis* by having supraciliary processes, much longer hind limbs (tibia length more than 60% of the snout–vent length), and prominent projections on the heels (two conical tubercles in *G. antomia*, and triangular calcars in *G. bufona* and *G. guentheri*). The remaining species, *G. trachyceps*, differs from *G. ossilaginis* by having the first and second fingers equal in length, instead of the first shorter than the second (as in *G. ossilaginis*); by lacking low tubercles on the heel; and in coloration, with pale labial and dorsolateral stripes present in *G. trachyceps* and absent in *G. ossilaginis*.

Description

The following description is based on four specimens. The body is moderately robust. The maximum known snout–vent length is 38.5 mm in males, and 53.3 mm in females. The head is wider than long, and as wide as the body. The snout is narrowly truncate in dorsal view, and in profile is bluntly rounded above and inclined anteroventrally. The canthus rostralis is straight, rounded in cross-section, and not elevated. The loreal region is slightly concave; the lips are rounded. The top of the head is slightly depressed between the elevated lateral edges of the frontoparietals, which form low cranial crests extending posteriorly nearly to the posterior end of the skull. The interorbital distance is about twice the width of the upper eyelid. The internarial area is flat. The nostrils are slightly protuberant, and are directed laterally at a level slightly posterior to the anterior margin of the lower jaw. The diameter of the eye is about equal to its distance from the nostril. The tympanum is nearly round; its diameter is about two-thirds the diameter of eye, and is separated from the eye by a distance nearly half again the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is inclined posteroventrally from the posterior end of the supratympanic crest, and obscures the upper edge of the tympanum.

The arm is moderately robust, and lacks ulnar tubercles. The hand is large. The fingers are long, and bear small rounded discs; the width of the disc on the third finger is about three-fourths the diameter of the tympanum. The relative lengths of the fingers are I < II < IV < III. The fingers are unwebbed. The palmar tubercle is small, low, and ovoid; the prepollical tubercle is large and elliptical. The subarticular tubercles are small and round; none are bifid. The supernumerary tubercles are large, prominent, and present only on the proximal segments of the digits; nuptial excrescences are present on the base of the thumb. The hind limb is moderately slender; when the hind limbs are adpressed, the heels overlap by about one-fourth the length of the tibia. The tibia length is about 50% of the snout–vent length; the foot length is about 51.0% of the snout–vent length. Calcars are absent; the heel bears two low diffuse tubercles. There are three low tubercles on the outer edge of the tarsus; an inner tarsal fold is absent. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is large, flattened, ovoid, and barely visible from above. The toes are long, and bear rounded discs about the same size as those on the fingers. The relative lengths of the toes are I < II < III < V < IV. The toes are about one-fourth webbed; the webbing formula is **I**2–2^+ **II**2–3**III**2–3^+**IV**3^+–2^+**V**. The subarticular tubercles are small and round; the supernumerary tubercles are prominent, subconical, and present only on the proximal segments of the digits.

The skin on the dorsum of the body and limbs is finely shagreen, with a few small tubercles on the forearms and hind limbs; the skin on the head is co-ossified with the underlying nasals, frontoparietals, and zygomatic and otic rami of the squamosal; the skin on the flanks is weakly areolate; the skin on the throat, chest, belly, and ventral surfaces of the forelimbs and thighs is coarsely areolate; the skin on the ventral surfaces of the shanks and tarsi is smooth. The opening of the brood pouch is U-shaped, at the level of the sacrum. Cloacal tubercles are absent. The dentigerous processes of the vomers are prominent, nearly transverse between the ovoid choanae, and narrowly separated medially. Each process bears five teeth.

COLOR IN PRESERVATIVE

The flanks and dorsal surfaces of the body and limbs are a nearly uniform pale gray. Narrow lines form incomplete irregular black circles, one each on the left side of body in the scapular region, and on the posterior part of the left flank. The anterior and posterior surfaces of the thighs are dark gray. The throat, chest, and anterior part of the belly are creamy gray; the posterior part of the belly and ventral surfaces of the thighs are grayish tan.

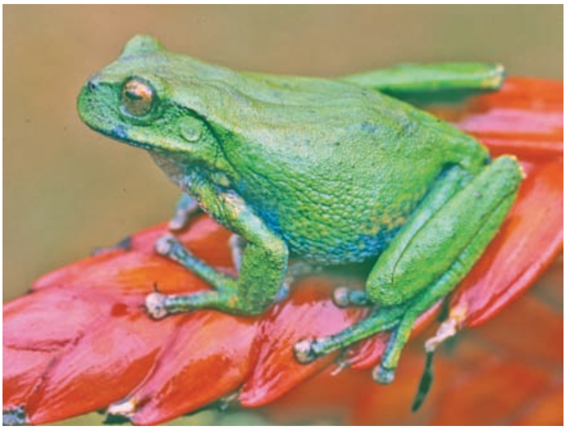

Fig. 12.31 *Gastrotheca ossilaginis* (KU 272294), female, 44.5 mm SVL, Lago Quindecocha, 3100 m, San Martín, Peru. Photo by P. Venegas, KUDA.

COLOR IN LIFE

In most individuals the dorsal surfaces of the head, body, and limbs are pale brown (Fig. 12.31). A broad darker brown middorsal mark extends posteriorly from the occipital region; the mark bifurcates into paravertebral marks just posterior to the scapula; these coalesce between the sacrum and cloacal region. The loreal and tympanic regions are pale brown; a dark brown post-tympanic stripe may be present. All ventral surfaces are pale gray. The iris is coppery brown, with fine darker reticulations. In one adult female all dorsal surfaces were bright green; a yellow patch was present in the inguinal region.

MEASUREMENTS

In all measurements except eye diameter, females are notably larger than males (Table 12.16).

CRANIAL OSTEOLOGY

Radiographs reveal some aspects of the cranial structure. The dermal roofing bones (nasals, dermal sphenethmoid, and frontoparietals) are deeply sculptured, and are co-ossified with the overlying skin. The nasals broadly articulate medially; their borders are not distinct from the dermal sphenethmoid. The frontoparietals have a complete articulation medially, and are in broad contact with the sphenethmoid. Each frontoparietal has an extensive supraorbital flange that is elevated, and is broadest at the level of the posterior part of the orbit; the otic flange of the frontoparietal does not articulate with the squamosal. A temporal arcade is absent. The otic and zygomatic rami of the

Table 12.16 Measurements for adults of *Gastrotheca ossilaginis*

	Males ($n = 2$)		Females ($n = 2$)	
Character	Mean	Range	Mean	Range
Snout–vent length	37.6	36.7–38.5	48.9	44.5–53.3
Tibia length	18.5	18.0–19.0	25.4	24.6–26.1
Foot length	17.2	17.1–17.3	24.8	21.7–25.8
Head length	13.3	13.2–13.4	17.0	16.7–17.3
Head width	13.5	13.4–13.6	18.5	17.5–19.5
Interorbital distance	6.6	6.6	7.6	7.4–17.8
Eyelid width	2.9	2.9	3.3	3.2–3.4
Internarial distance	2.5	2.4–26	2.9	2.8–3.0
Eye diameter	4.5	4.4–4.6	4.1	3.7–4.5
Eye–nostril distance	3.7	3.6–3.8	4.4	4.2–4.6
Orbit–jaw distance	1.8	1.8	3.1	2.9–3.3
Nostril–jaw distance	2.7	2.6–2.8	3.7	3.6–3.8
Tympanum diameter	2.3	2.3	2.9	2.8–3.0
Thumb length	6.5	6.4–6.8	9.5	8.8–10.2
Third finger length	12.0	11.9–12.1	17.3	16.5–18.1
Disc width	1.8	1.7–1.9	2.2	2.1–2.3

squamosal are robust; the latter appears to articulate with the maxilla.

Life History

The eggs hatch as froglets. On 20 November, a brown female having a snout–vent length of 53.3 mm gave birth to 21 young, each about 7.4 mm in snout–vent length. About half the hatchlings were brown, and the others were green. On 26 November, another brown female produced 14 brown froglets.

Advertisement Call

The call is unknown.

Distribution and Ecology

Gastrotheca ossilaginis is known only from two localities, at elevations of 3000–3100 m in the vicinity of Lago de los Cóndores in the northern part of the Cordillera Central in Departamento de Amazonas in northern Peru (Fig. 12.12). Three individuals were found at night on low bushes and a spiny terrestrial bromeliad; one was under a rock in a pasture by day.

Conservation Status

This species is categorized as Data Deficient in the IUCN Red List.

Etymology

According to Duellman and Venegas (2005), the specific name *ossilaginis* is a Latin adjective meaning "bony hardness"; the name refers to the bony nature of the integumentary cranial co-ossification.

Remarks

The skull of *Gastrotheca ossilaginis* is similar to that of *G. abdita*, a species restricted to the adjacent Cordillera Colán. Both species have large nasals in broad median contact, nasals and frontoparietals in broad contact with the dermal sphenethmoid, and frontoparietals with supraorbital flanges. The two species differ in that the dermal roofing bones in *G. abdita* are not co-ossified with the overlying skin, and the supraorbital flanges are narrower than those in *G. ossilaginis*.

Gastrotheca (*Gastrotheca*) *pacchamama* Duellman

Gastrotheca pacchamama Duellman, 1987:905.—Holotype: KU 163288 from N slope Abra Tapuna, 7 km [by road] N Mahuayara, 3710 m, Región de Ayacucho, Peru.

Diagnosis

This moderately small species attains a snout–vent length of 38.0 mm. The tibia length is less than 50% of the snout–vent length, and is slightly shorter than the foot. The interorbital distance is slightly greater than the width of the upper eyelid. The skin on the dorsum is smooth (pustular laterally), not co-ossified with skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is shorter than the second. The discs on the fingers are slightly wider than the digits proximal to the discs. The fingers are unwebbed; on the toes the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is tan, gray, red, or brown, usually with a darker middorsal mark or paravertebral marks. Markings on the head consist of a pale labial stripe, dark canthal stripe, and (usually) dark interocular bar. A pale dorsolateral stripe is absent. The flanks are uniformly pale gray; the venter is tan, with or without dark flecks.

Gastrotheca pacchamama is most like *G. excubitor*, *griswoldi*, and *rebeccae* in size and general structure. It resembles *G. rebeccae* in having an acutely rounded snout in dorsal view, but is unlike that species in profile, with a snout that strongly projects well beyond the anterior margin of the lower lip, in contrast to a bluntly rounded snout that barely protrudes beyond the jaw in *G. rebeccae*. Furthermore, the dorsum usually lacks a dark longitudinal middorsal mark in *G. pacchamama*, whereas middorsal marks usually are present in the other species. *G. pacchamama* also differs by having proportionately shorter legs; the tibia length is only about 45% of the snout–vent length, in comparison with 51% in *G. rebeccae*. *G. excubitor* differs by having a much broader interorbital distance ($\bar{x}$ = 189% of eyelid width) than *G. griswoldi* ($\bar{x}$ = 117%), *G. pacchamama* ($\bar{x}$ = 125%), or *G. rebeccae* ($\bar{x}$ = 150%). *G. ochoai* is superficially similar to *G. pacchamama*, but *G. ochoai* is smaller (males to 30.4 mm, females to 37.5 mm) and has tubercular skin on the dorsum.

Description

The following description is based on 27 specimens. The body is moderately robust. The maximum snout–vent length is 37.0 mm in males, and 38.0 mm in females. The head is slightly wider than long, and nearly as wide as the body. The snout is acutely rounded in dorsal view; in profile the snout is bluntly rounded, and extends well beyond the margin of the lower lip. The canthus rostralis is rounded in cross-section. The loreal region is barely concave; the lips are rounded. The top of the head is flat. The interorbital distance is 125%–150% of the width of the upper eyelid. The internarial area is flat. The nostrils are not protuberant, and are directed laterally at the anterior terminus of the canthus rostralis at the level of the anterior margin of the lower jaw. The diameter of the eye is about equal to the distance from the eye to the nostril. The tympanum is vertically ovoid, and is separated from the eye by a distance equal to the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately heavy, obscures the upper part of the tympanum, and extends from the posterior corner of the orbit to a point above the insertion of the forelimb.

The arm is moderately robust; ulnar tubercles are absent. The hand is small. The fingers are unwebbed. The discs on the fingers are small and subtruncate; the width of the disc on the third finger is equal to the length of the tympanum. The relative lengths of the fingers are I < II < IV < III. The subarticular tubercles are moderately large and subconical; the distal tubercle on the fourth finger is weakly bifid in some specimens. The supernumerary tubercles are small, subconical, and numerous on the proximal segments. The palmar tubercle is trifid, and forms three distinct tubercles; the prepollical tubercle is elongate; the thumb bears small nuptial excrescences in breeding males. The hind limb is robust. The tibia length is about 45% of the snout–vent length; the foot length is about 46% of the snout–vent length. Calcars and an outer tarsal fold are absent; an inner tarsal fold extends the length of the tarsus. Numerous low tubercles are present on the ventral surface of the tarsus. The outer metatarsal tubercle is small and conical; the inner metatarsal tubercle is elliptical, and is barely visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III = IV < V. The toes are no more than about one-third webbed. Webbing is absent between the first three toes; the webbing formula for the outer toes is **IV**(3–4)—(2–3)**V**. The subarticular tubercles are small and subconical; the supernumerary tubercles are minute, and are numerous on the proximal segments of the toes.

The skin on the top of the head, middorsum of the body, and dorsal surfaces of the limbs is smooth; other dorsal surfaces and the flanks are pustular; the skin on the ventral surfaces of the shanks is smooth; the other ventral surfaces are granular. A pair of vertically elliptical tubercles lies below the cloacal opening. The opening of the brood pouch is narrowly U-shaped, with the anterior border just posterior to the sacrum. The dentigerous processes of the vomers are inclined posteromedially; they nearly abut medially between the small round choanae. Each process bears five to seven teeth.

COLOR IN PRESERVATIVE

The dorsal surfaces are dull grayish brown or pale brown, usually (97%) with dark marks on the dorsum of the body (Fig. 12.32). The dark marks on the body consist of an interorbital bar (78%), longitudinal paravertebral marks (43%; Fig. 12.32B), a broad middorsal mark (20%; Figs. 12.32C and D, narrow middorsal mark (13%; Fig. 12.32E), and/or spots or plain (8%; Fig. 12.32A). A narrow creamy white canthal stripe continues onto the outer edge of the eyelid and then onto the supratympanic fold; it is bordered below in the loreal region by a narrow dark brown stripe. The postorbital region is dark brown; the flanks are pale gray. The limbs are colored like the dorsum of body, and have faintly darker transverse bars: two on the forearm, and three each on the thigh, shank, and tarsus. The anterior and posterior surfaces of the thighs and inner surfaces of the shanks are brown; the subcloacal tubercles are creamy white; the venter is grayish tan.

COLOR IN LIFE

In individuals from Abra Tapuna, Región de Ayacucho, Peru, the dorsum is either uniformly bright rust or tan,

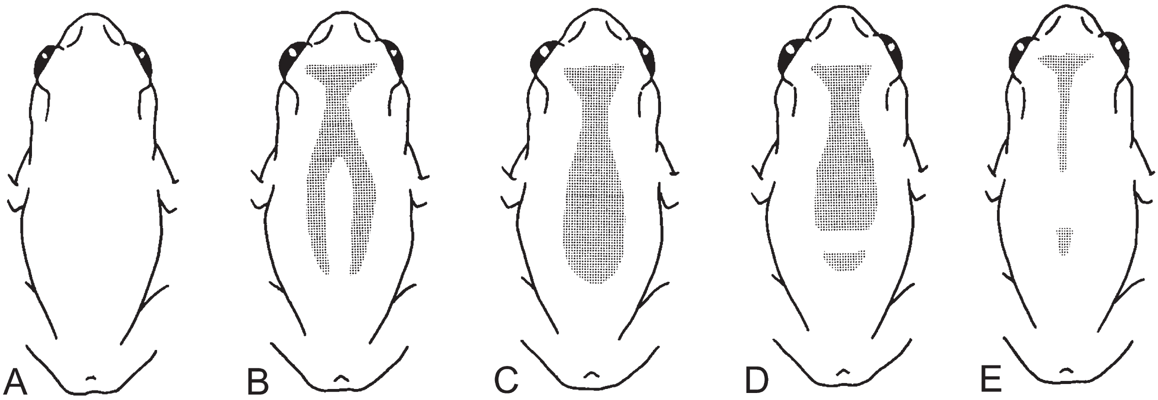

Fig. 12.32 Diagrammatic representative types of the dorsal color patterns in *Gastrotheca pacchamama*.

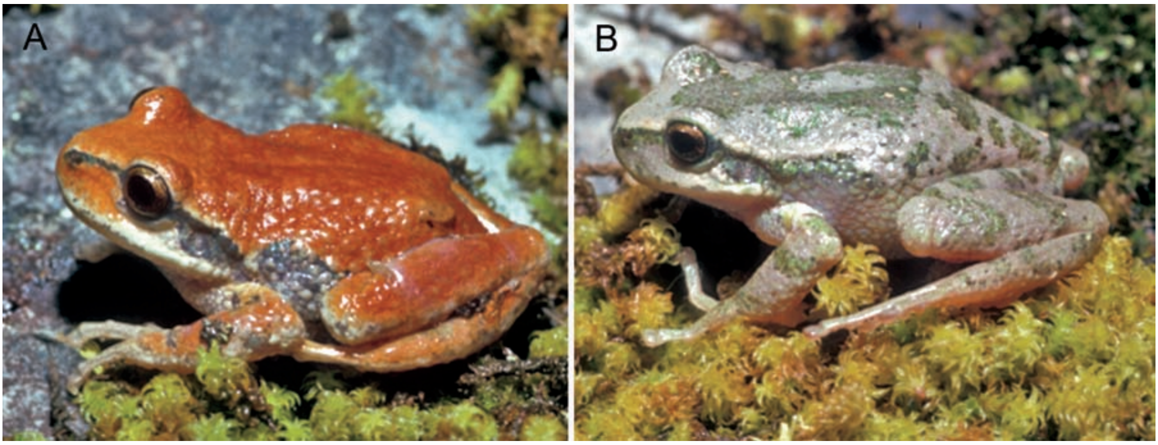

Fig. 12.33 *Gastrotheca pacchamama*. A: KU 163281, female, 33.3 mm SVL. B: KU 163282, female, 33.4 mm SVL. Both from Abra Tapuna, 3710 m, Ayacucho, Peru. Photos by W. E. Duellman.

or gray, tan, or pale green with olive-brown to green markings. The canthal and supratympanic stripes are cream to bronze tan; the labial stripe is cream to yellowish tan. The postorbital bar is green, and extends to midflank in some individuals. The upper flanks have brown spots in some individuals (Fig. 12.33); the lower flanks and belly are gray, with a blue tint in the axilla and groin in some. The posterior surfaces of the thighs are pinkish brown. The throat is dull pinkish cream; the ventral surfaces of the limbs are pink. The iris is bronze, with fine black reticulations. Small creamy yellow pustules are scattered on the dorsum in some individuals (W. E. Duellman field notes, 22 February 1975).

MEASUREMENTS

Females are only slightly larger than males (Table 12.17).

CRANIAL OSTEOLOGY

The dermal roofing bones are not co-ossified with the overlying skin. The sphenethmoid is sculptured. The nasals articulate medially; their borders are distinct from the sphenethmoid. The frontoparietals have an incomplete articulation medially, and lack supraorbital and otic flanges. A temporal arcade is absent. The carotid canal is open. The preorbital process is not separated by a notch from the facial process of the maxilla; a postorbital process is absent. The head of the squamosal has a narrow crest; the zygomatic ramus extends more than halfway to the maxilla. The otic ramus of the squamosal completely articulates with and moderately overlaps the ossified crista parotica; an auxiliary dorsal ramus is absent. The parasphenoid has an attenuate posteromedian process; the cultriform process terminates posterior to the level of the neopalatines. The parasphenoid alae do not

Table 12.17 Univariate statistics for adults of *Gastrotheca pacchamama* and *G. rebeccae*

		G. pacchamama (9 males, 6 females)			*G. rebeccae* (26 males, 25 females)		
Character	Sex	Mean	Range	SD	Mean	Range	SD
Snout–vent length	males	35.8	34.9–37.0	0.80	35.7*	30.6–44.7	3.76
	females	36.5	34.5–38.0	1.34	39.9*	33.1–45.7	3.21
Tibia length	males	16.0	15.1–16.9	0.57**	17.9	12.4–22.3	2.31
	females	16.5	15.9–16.8	0.35**	20.8	17.8–23.7	1.78
Foot length	males	16.6	15.5–17.7	0.68	16.4	12.4–21.5	2.50
	females	16.6	15.9–17.2	0.49	18.9	15.4–22.7	1.80
Head length	males	13.6	11.6–15.5	1.53	12.4*	10.9–15.8	1.27
	females	13.4	11.9–14.7	1.42	13.6*	11.8–15.3	0.97
Head width	males	13.1	12.7–13.5	0.24**	13.6	12.0–16.0	1.13
	females	13.1	12.6–13.9	0.45**	15.2	13.1–17.3	1.13
Interorbital distance	males	4.4	3.8–5.0	0.35**	4.8	4.1–6.6	0.69
	females	4.7	4.3–5.0	0.24**	5.3	4.2–6.4	0.57
Eyelid width	males	3.5	3.1–3.8	0.24	3.2	2.7–4.3	0.33
	females	3.6	3.2–4.1	0.34	3.3	2.8–4.4	0.35
Internarial distance	males	2.4	2.2–2.7	0.19	2.3	1.9–2.8	0.26
	females	2.2	1.8–2.4	0.25	2.5	2.1–3.0	0.24
Eye diameter	males	3.4	2.9–3.7	0.27**	3.5	2.8–4.5	0.48
	females	3.4	3.0–3.9	0.31**	3.6	1.9–4.1	0.34
Eye–nostril distance	males	3.4	3.0–3.8	0.29	3.6	3.2–4.5	0.40
	females	3.6	3.2–3.8	0.24**	4.0	3.4–4.8	0.36
Orbit–jaw distance	males	2.4	2.2–2.7	0.22	1.7	1.4–2.5	0.29
	females	2.2	1.7–2.5	0.30	1.9	1.5–2.6	0.28
Nostril–jaw distance	males	2.6	2.2–2.9	0.19	2.9*	2.3–3.5	0.26
	females	2.6	2.2–2.9	0.24	3.3*	2.9–3.8	0.26
Tympanum diameter	males	1.8	1.2–2.1	0.25	1.8	1.4–2.7	0.31
	females	1.7	1.4–2.0	0.22	1.8	1.3–2.4	0.23
Thumb length	males	5.6	4.8–6.4	0.45**	6.1	4.1–8.9	1.05
	females	5.7	5.5–6.0	0.20**	6.7	5.9–8.0	0.65
Third finger length	males	10.9	10.3–11.3	0.30**	11.5	9.7–14.7	1.36
	females	11.0	10.4–11.5	0.41**	12.7	10.6–15.3	1.31
Disc width	males	1.2	1.0–1.5	0.17**	1.8	1.3–2.6	0.26
	females	1.3	1.1–1.5	0.16**	2.2	1.8–2.6	0.29

*Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

**Differences between the means of the two species are significant (ANOVA, $P \leq 0.01$).

articulate with the pterygoids. The neopalatines have a smooth ventral ridge, and are moderately separated medially; they do not form the posterior margins of the choanae. The pterygoid articulates with the squamosal; the median ramus of the pterygoid is not expanded medially; an auxiliary dorsal ramus is present.

Life History

No brooding females with developing embryos exist in collections, but the size and number of ovarian eggs are indicative of direct development. Four females collected at Abra Tapuna on 22 February 1975 have snout–vent lengths of 35.1–38.0 mm ($\bar{x} = 36.9$) and contained 5–8 ovarian eggs ($\bar{x} = 6.3$) with diameters of 4.7–5.5 mm ($\bar{x} = 5.1$). These data strongly suggest that *Gastrotheca pacchamama* has direct development.

Advertisement Call

No recordings are available.

Distribution and Ecology

This species is known only from wet grassland above treeline at the crest of the Cordillera Oriental in Región de Ayacucho, Peru (Fig. 12.34). In February 1975 at Abra Tapuna (3710 m), individuals were found under rocks in wet grassland; some males were calling during the day from moss-covered talus. At that time the air temperature was 13.0°C–17.5°C, and the temperature under the rocks was 9.0°C–10.5°C.

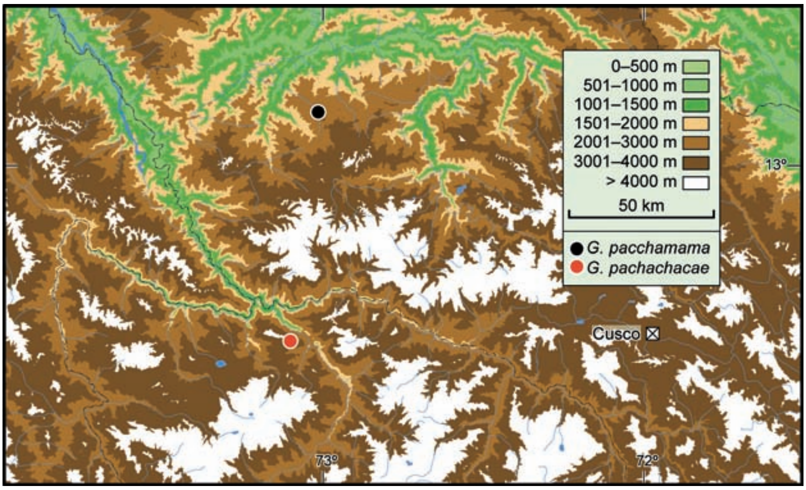

Fig. 12.34 Andean region of southcentral Peru, showing the localities of known occurrences of *Gastrotheca pacchamama* and *G. pachachacae*.

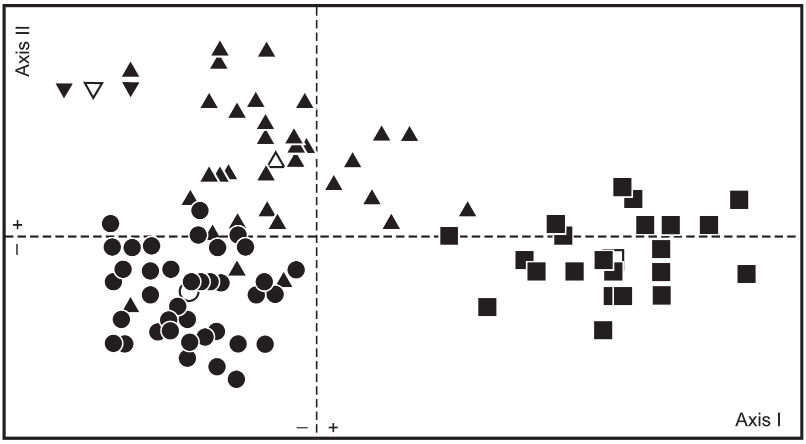

Fig. 12.35 Multivariate plot of a stepwise discriminant analysis of morphometrics of two species of *Gastrotheca* in the Cordillera Oriental of central Peru. Squares = *G. pacchamama* from Abra Tapuna (n = 23). Other symbols = *G. rebeccae*: inverted triangles = from Cano (n = 2), triangles = from Mitupucuru-Yuraccyacu (n = 36), circles = from Yanamonte (n = 40). Open symbols = means of the samples.

Conservation Status

This species is categorized as Data Deficient in the IUCN Red List.

Etymology

The specific name is a noun in apposition. In the Quecchuan language, *paccha* means "earth" and *mama* means "mother." Pacchamama is a Quecchuan Indian mythical goddess of the high places (*abras*); according to custom and myth, Quecchuans place piles of stones at high places and, during journeys, leave food beneath the stones for Pacchamama to ensure a safe journey for themselves. Some of the type series of this species was found under one of these piles of stones at Abra Tapuna (Duellman, 1987).

Remarks

Formerly, this species was confused with *G. rebeccae*. Duellman and Trueb (1988) showed the existence of differences in several cranial features—e.g., robustness of the crista parotica, separation of the frontoparietals, degree of separation of the neopalatines, and shapes of the vomers. Subsequently, minor external differences were noted. The morphometric characters of the two species are summarized in Table 12.17, and the results of a stepwise discriminant analysis of morphometrics is shown in Fig. 12.35.

Gastrotheca (Gastrotheca) pachachacae Catenazzi and von May

Gastrotheca pachachacae Catenazzi and von May, 2011:162.
Holotype: MUSM 38489 from Chinchay, 3050 m, Distrito Pacobamba, Provincia de Andahuaylas, Región de Apurímac, Peru.

Diagnosis

This small species attains a snout–vent length of 35.3 mm. The tibia length is about 50% of the snout–vent length, and is barely longer than the foot. The interorbital distance is slightly greater than the width of the upper eyelid. The skin on the dorsum is granular, not co-ossified with skull, and lacks transverse ridges. Supraciliary processes are absent. The heel bears a small calcar. The tympanic annulus is smooth. The first finger is slightly shorter than the second. The discs on the fingers are slightly wider than the digits proximal to the discs. The fingers are unwebbed; on the toes, the webbing extends maximally to a point midway between the antepenultimate and penultimate subarticular tubercles on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is pale brown, with a few small dark brown flecks. Dark markings on the head and a pale dorsolateral stripe are absent. The flanks are pale brown, with dark brown flecks; the axilla and groin are bluish green; the venter is uniformly cream.

Among the small to moderate-sized species of *Gastrotheca* on the eastern slopes of the Andes from northern Peru southward, *G. pachachacae* is most like *G. abdita*, *ochoai*, and *zeugocystis* in lacking dark markings (i.e., canthal and postorbital stripes, and an interocular bar). *G. abdita* differs from *G. pachachacae* by having a conical tubercle on the heel, Fingers I and II equal in length, and smooth skin on the dorsum; *G. ochoai* differs by having an acuminate snout in dorsal view, an interorbital distance half again the width of the upper eyelid, tubercular skin on the dorsum, and no calcar. Likewise, *G. zeugocystis* lacks a calcar, has Fingers I and II equal in length, and has lateral brooding pouches, as does *G. antoniiochoai*; the latter species is like *G. pachachacae* in lacking canthal and postorbital stripes and an interocular bar. The slightly larger *G. atympana* differs from *G. pachachacae* by lacking a tympanum and by having a row of tubercles on the heel and a brown interocular bar. Four much larger species inhabiting lower elevations (*G. andaquiensis*, *longipes*, *testudinea*, and *weinlandii*) also differ from *G. pachachacae* by having the first finger much longer than the second. All other species of *Gastrotheca* in this region (*G. christiani*, *chrysosticta*, *excubitor*, *gracilis*, *nebulanastes*, *pacchamama*, *piperata*, and *rebeccae*) differ from *G. pachachacae* by having dark markings on the head (usually canthal and postorbital stripes and an interocular bar) as well as longitudinal markings on the dorsal surfaces of the body and transverse bars on the limbs.

Description

The following description is based on three specimens. The body is moderately robust. The maximum known snout–vent length is 29.3 mm in males, and 35.3 mm in the only known female. The head is slightly wider than long, and about as wide as the body. The snout is rounded in dorsal view, and bluntly rounded to nearly truncate in profile. The canthus rostralis is rounded in cross-section. The loreal region is barely concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 118% of the width of the upper eyelid. The internarial area is flat. The nostrils are slightly protuberant, and are directed anterolaterally at the anterior terminus of the canthus rostralis at the level of the anterior margin of the lower jaw. The diameter of the eye is slightly less than the distance from the eye to the nostril. The tympanum is round, and is separated from the eye by a distance greater than the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately heavy and tuberculate, obscures the upper part of the tympanum, and extends from the posterior corner of the orbit to a point above the insertion of the forelimb.

The arm is moderately robust; ulnar tubercles are absent. The hand is moderately large. The fingers are unwebbed. The discs on the fingers are small, and are broadly rounded; the width of the disc on the third finger is equal to about two-thirds the length of the tympanum. The relative lengths of the fingers are I < II < IV < III. The subarticular tubercles are moderately large and subconical; none are bifid. The supernumerary tubercles are small, subconical, and present only on the proximal segments. The palmar tubercle is indistinct; the prepollical tubercle is elongately elliptical; the thumb bears brown nuptial excrescences in breeding males. The hind limb is moderately slender. The tibia length is about 50% of the snout–vent length, and is barely longer than the foot. Calcars and tubercles are absent on the heel. An inner tarsal fold is absent. The outer metatarsal tubercle is small and round; the inner metatarsal tubercle is elongate, elevated, and visible from above. The toes are slender. The relative lengths of the toes are I < II < III < IV < V. The toes are less than one-fourth webbed. The webbing formula is **I**2½—2½**II**2—3^{+}**III**3^{-}—3½**IV**(3^{+}—2½)**V**. The subarticular tubercles are moderately large and subconical; the supernumerary tubercles are small, subconical, and present only on the proximal segments of the toes.

The skin on the dorsal surfaces is finely granular; the skin on the flanks, posteroventral surfaces of the thighs, and belly is coarsely granular; the skin on the throat and ventral surfaces of the shanks is smooth. A pair of conical tubercles lies below the cloacal opening. The opening of the brood pouch is U-shaped, with the anterior border just posterior to the sacrum. The dentigerous processes of the vomers are transverse, and are narrowly separated medially at a level slightly posterior to the small ovoid choanae. Each process bears three or four teeth.

COLOR IN PRESERVATIVE

The dorsum is gray, with a few small darker flecks; the transverse bars on the limbs are barely visible. The canthal and postorbital stripes are diffuse dark brown, bordered by cream; the tympanum is brown. The flanks are gray to pale brown, with black flecks. Dorsally, Toes IV and V are gray; the inner toes are cream. The tubercles below the cloaca are white; the ventral surfaces are cream.

COLOR IN LIFE

Catenazzi and von May (2011:164; also see Fig. 12.36 herein) described the coloration of the holotype: "Dorsal surfaces of head and body pale brown to golden, with few small dark flecks and no interorbital bar. The middle part of the flanks is similar in coloration to the dorsum but have dark flecks, whereas the axillary and inguinal regions have diffuse bluish coloration with green tones. The venter is cream without marks; the ventral surfaces of the limbs are pink. The canthal and supratympanic [postorbital] stripes are diffuse and dark brown, bordered with cream. The tympanum is brown. The margin of the upper eyelid is cream. The iris is bronze with black reticulations and the periphery is black. The bones are white." A juvenile has diffuse brown spots on a cream belly.

MEASUREMENTS

The single female is slightly larger than the males. From data provided by Catenazzi and von May (2011), the measurements (in mm) of two males are followed by those of one female: snout–vent length 28.7, 29.2, 35.3; tibia length 14.5, 14.5, 17.5; foot length 14.3, 14.1, 17.3; head length 10.0, 10.2, 11.5; head width 10.6, 10.7, 12.0; interorbital distance 3.3, 3.4, 4.0; eyelid width 2.7, 2.9, 3.5; internarial distance 2.7, 2.8, 2.9; eye diameter 3.4, 3.5, 3.6; eye–nostril distance 3.4, 3.5, 4.2; orbit–jaw distance 1.3, 1.3, 1.5; nostril–jaw distance 2.0, 2.2, 2.6; tympanum diameter 1.8, 1.8, 2.0; thumb length 5.0, 5.3, 6.5; third finger length 9.4, 9.5, 11.2; and width of disc on third finger 1.1, 1.2, 1.4.

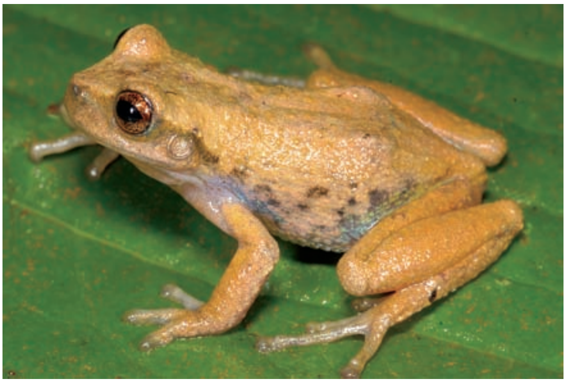

Fig. 12.36 *Gastrotheca pachachacae* (MUSM 28490), male, 28.7 mm SVL, Chinchay, 3050 m, Distrito Pacobamba, Provincia Andahuaylas, Apurímac, Peru. Photo by A. Catenazzi, KUDA.

CRANIAL OSTEOLOGY

No data are available.

Life History

Nothing is known.

Advertisement Call

Catenazzi and von May (2011) reported results of an analysis of 25 calls of a single male. The call consists of a single note 956–1476 milliseconds ($\bar{x} = 1.294.4 \pm 132.3$) in duration, containing 39–58 pulses ($\bar{x} = 48.9 \pm 5.2$). The call frequency is 8.8–14.3 calls per minute ($\bar{x} = 11.2 \pm 2.3$), with intervals of 2.37–7.20 milliseconds ($\bar{x} = 3.74 \pm 1.147$) between calls. The fundamental frequency is dominant and ranges from 2.173 to 2.438 Hz (median = 2.279).

Distribution and Ecology

Gastrotheca pachachacae is known only from the type locality, an isolated patch of about 2000 hectares of cloud forest on steep slopes in the upper watershed of a tributary of the Río Pachachaca, north of Río Apurimac, in the Cordillera Oriental in southcentral Peru (Fig. 12.34). All individuals were perched on vegetation at night; the frogs may use the abundant bromeliads as diurnal shelters.

Conservation Status

The status of *Gastrotheca pachachacae* has not been determined in the IUCN Red List. Catenazzi and von May (2011) noted that conservation efforts for the isolated cloud forest are being promoted by local authorities.

Etymology

As stated in the original description (Catenazzi and von May, 2011), the specific name *pachachacae* refers to Río Pachachaca, a tributary of Río Apurímac in southern Peru. The type locality is an area of cloud forest in the upper drainage of the river.

Remarks

In a phylogenetic analysis of molecular data, *Gastrotheca pachachacae* was in a clade with several other species inhabiting puna and areas of cloud forest in central and southern Peru. Females of these species—*G. atympana*, *excubitor*, *nebulanastes*, and *ochoai*—all produce a few large eggs that undergo direct development; presumably *G. pachachacae* does the same.

Gastrotheca (*Gastrotheca*) *peruana* (Boulenger)

Nototrema peruana Boulenger, 1900:181.—Syntypes: BMNH 1947.2.22.42–46 from "Carao" [= Caraz], Región de Ancash, Peru.

Gastrotheca peruana peruana—Vellard, 1957:27.

Gastrotheca peruana dissimilis—Vellard, 1957:30.—Syntypes: MUSM 245 (47 specimens) from Huamachuco, Región de La Libertad, Peru. Type series recatalogued and MUSM 7740 designated as lectotype by Morales et al. (1990). Synonymy fide Duellman and Fritts, 1972:11.

Gastrotheca peruana junensis—Vellard, 1957:32.—Holotype: MUSM 195 (3 specimens) from Lago de Punrún, Región de Pasco, Peru. Type series recatalogued and MUSM 1595 designated as lectotype by Morales et al. (1990). Synonymy fide Duellman and Fritts, 1972:11.

Gastrotheca peruana—Duellman and Fritts, 1972:11.

Gastrotheca (*Gastrotheca*) *peruana*—Dubois, 1987:33.

Diagnosis

This medium-sized species attains a maximum snout–vent length of 56.5 mm. The tibia length is less than 45% of the snout–vent length, and is about as long as the foot. The interorbital distance is about equal to the width of the upper eyelid. The skin on the dorsum is pustular, not co-ossified with skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is granular. The first and second fingers are equal in length. The discs on the fingers are slightly wider than the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is gray, green, or tan, usually with darker paravertebral marks. Markings on the head consist of a pale labial stripe and dark canthal stripe. A pale dorsolateral stripe is absent. The flanks are tan or gray, with or without dark spots. The venter is tan, with or without dark flecks.

Gastrotheca peruana is like *G. phalarosa* in having an inclined protruding snout in profile, interorbital distance about equal to the width of the upper eyelid, and pustular skin on the dorsum. *G. peruana* differs from *G. phalarosa* (conditions of the latter in parentheses) by having an acutely rounded snout in dorsal view (nearly truncate), nostrils at the level of the anterior margin of the lower jaw (posterior to margin), tympanic annulus that is distinct and granular (barely evident and smooth), inner tarsal fold extending the full length of the tarsus (evident only distally), and in coloration: broad black canthal stripe (narrow white stripe), pale labial stripe (absent), and tan venter with or without brown flecks (black with white spots). *G. peruana* also resembles *G. griswoldi* and *G. marsupiata*, but differs from both by having the snout acutely rounded in dorsal view and inclined in profile (bluntly rounded in the other two species), pustular skin on the dorsum (granular in *G. griswoldi*), a proportionately narrower interorbital distance (110%–120% of width of upper eyelid in the other two species); first and second fingers equal in length (as opposed to first finger shorter than the second), and lacking a dark interocular bar (present in *G. griswoldi* and *G. marsupiata*).

Description

The following description is based on 100 specimens. The body is robust; the maximum snout–vent length is 52.6 mm in males, and 56.5 mm in females. The head is slightly wider than long, but not as wide as the body. The snout is acutely rounded in dorsal view, and convexly inclined from the nostrils to the tip in profile; the snout protrudes beyond the anterior margin of the lower jaw. The canthus rostralis is acutely rounded in cross-section. The loreal region is concave; the lips are rounded. The top of the head is flat. The interorbital distance is equal to the width of the upper eyelid. The internarial area is flat. The nostrils are not protuberant, and are directed anterolaterally at the terminus of the canthus rostralis at a point above the anterior margin of the lower jaw. The diameter of the eye is slightly greater than its distance from the nostril. The tympanum is round, and is separated from the eye by a distance about equal to the length of the tympanum. The tympanic annulus is distinct and granular. The supratympanic fold is heavy, obscures the upper and posterior margins of the tympanum, and extends from the posterior corner of the orbit to the angle of the jaw.

The arm is moderately robust, and lacks ulnar tubercles. The hand is small. The fingers are moderately long, and bear small round discs; the width of the disc on the third finger is much less than the length of the tympanum. The relative lengths of the fingers are I =

II < IV < III. The fingers are unwebbed. The subarticular tubercles are large and round; the supernumerary tubercles are large, round, and numerous proximally. The palmar tubercle is bifid; the prepollical tubercle is elliptical; the thumb bears a brown nuptial excrescence in breeding males. The hind limb is robust. The tibia length is about 42% of the snout–vent length; the foot length is about 43% of the snout–vent length. A calcar and tarsal tubercles are absent. A distinct curved inner tarsal fold extends the full length of the tarsus. The outer metatarsal tubercle is low and round; the inner metatarsal tubercle is elliptical, and is visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III = IV < V. The toes are about one-fourth webbed; the webbing formula is **I**2^+—2^+**II**(2^-–2)—(3–3^+)**III**(2–2^+)–(3–3^+)**IV**(3–3^+)—(2–2^+)**V**. The subarticular tubercles are large and round; the supernumerary tubercles are low, round, and present only on the proximal segments.

The skin on the dorsum is pustular; the skin on the flanks, belly, ventral surfaces of the forearms, thighs, and tarsi, and in the tympanic region is coarsely granular; the other surfaces are smooth. Cloacal folds and tubercles are absent. The opening of the brood pouch is narrowly U-shaped, with the anterior margin is at the level of the sacrum. The dentigerous processes of the vomers are posteromedially inclined, and narrowly separated medially between the choanae. Each process bears three to seven teeth.

COLOR IN PRESERVATIVE

The dorsum is gray or brown, usually (96%) with darker brown markings (usually narrowly edged with darker brown and narrowly bordered by cream) consisting of a pair of irregular continuous or interrupted longitudinal marks extending from the eyelids to the sacral region (where they are fused in 28% of the specimens), irregular spots between the sacrum and the vent, a dorsolateral row of spots (partially coalesced in some specimens) from the postorbital mark to the inguinal region (26%), and two or three transverse bars on each forearm, thigh, shank, and tarsus. Dark flecks are present lateral to the longitudinal marks on the dorsum in 26% of the specimens. A pale creamy gray labial stripe extends from a point below the orbit to the angle of the jaw (91%); a dark brown to black canthal stripe is present. The flanks are either uniformly tan or gray (62%) or have small dark brown spots (38%). The posterior surfaces of the thighs are uniformly creamy tan; the anterior surfaces of the thighs are uniformly tan (93%) or have grayish-brown mottling (7%). The venter is uniformly tan (72%) or has brown flecks (28%). A dark patch and a pale stripe and spots are absent in the cloacal region. The outer toes are colored like the inner ones. Many juveniles are uniformly brown or gray above and creamy tan below.

COLOR IN LIFE

The dorsum is green, gray, tan, or brown, usually with darker brown markings (Fig. 12.37). It is evident from the following descriptions that the coloration in living individuals of *Gastrotheca peruana* is highly variable, and that there are ontogenetic differences in the coloration of the groin and posterior surfaces of the thighs.

KU 212068 and MUSM 6114 from 26 km NNW Cajamarca, Región de Cajamarca, Peru.—The dorsum is bright green with metallic bronze dorsal markings on one specimen, and the other is pale tan with dark brown dorsal markings. The groin and hidden surfaces of the thighs are pale bluish green (W. E. Duellman field notes, 17 January 1989).

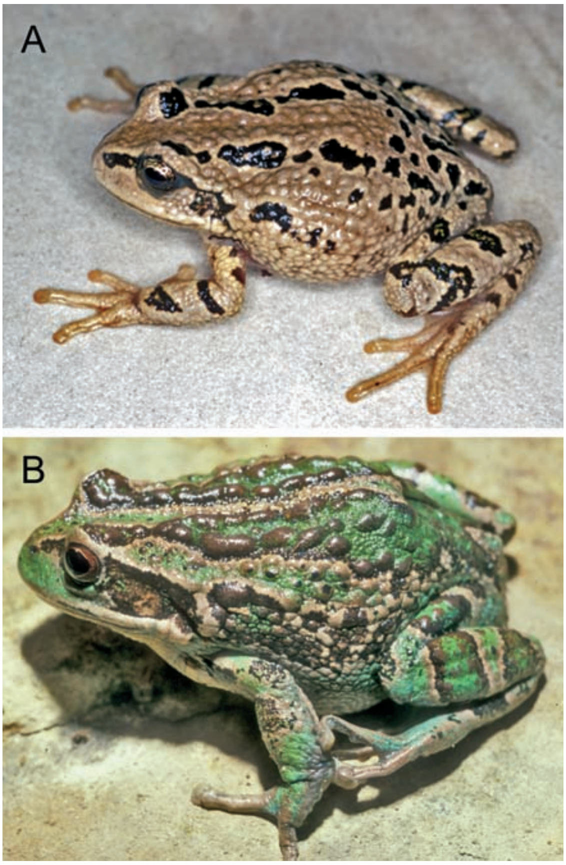

Fig. 12.37 *Gastrotheca peruana*. A: KU 139189, female, 37.7 mm SVL, 10 km S Carhuamayo, 4050 m, Junín, Peru. B: KU 212068, female, 55.4 mm SVL, 26 km NNW Cajamarca, Cajamarca, Peru. Photos by W. E. Duellman.

KU 212070 from 8 km S Cajamarca, Región de Cajamarca, Peru.—The dorsum is tan, with dark reddish-brown spots. The venter is creamy yellow. There is a tinge of blue in the groin and on the hidden surfaces of the hind limbs. The iris is reddish copper, with fine black flecks (W. E. Duellman field notes, 19 January 1989).

KU 138460–93 from 12 km E Huamachuco, Región de La Libertad, Peru.—The dorsum is beige, pale brown, or gray brown; darker individuals have dark brown blotches and prominent bars on the limbs; paler ones have beige, tan, or gray blotches on the body and indistinct bars on the limbs. The posterior surfaces of the thighs are dark brown to flesh beige, with white flecks in darker individuals. About half the individuals have pink or orange blotches in the inguinal region and on the posterior surfaces of the thighs. The iris is metallic red (T. H. Fritts field notes, 16 April 1970).

KU 138495–512 from Chiquián, Región de Ancash, Peru.—The dorsum of the adults is pale gray, bronze tan, or dark gray brown to medium brown; most have dark brown or dark bronze-brown blotches on the body and transverse bars on the limbs. The anterior and posterior surfaces of the thighs are dark brown. The inguinal region and posterior surfaces of the thighs of 10 specimens have conspicuous orange blotches; one adult female has a slight orange tint on the distal posterior surfaces of the thighs. Seven juveniles have white to yellow spots in the inguinal region and on the posterior surfaces of the thighs. The iris is reddish bronze (T. H. Fritts field notes, 2 April 1970).

KU 138527–44 from 5 km N Recuay, Región de Ancash, Peru.—The dorsum is gray, grayish tan, or medium brown in adults (one female has dorsal coloration nearly obscured by a yellowish-green suffusion). The dorsal blotches are yellowish green, yellowish tan, or medium brown outlined in black. Four of the six adults have an orange tint or orange blotches on the posterior surfaces of the thighs; in the others the posterior surfaces of the thighs are either dark brown with beige flecks, or gray or beige with dark brown blotches. In adults the inguinal region and anterior surfaces of the thighs lack orange coloration. Juveniles are grayish beige to medium brown, with green or dark brown blotches; the inguinal region and posterior surfaces of the thighs are dark brown, with reddish-orange blotches. The iris is reddish bronze (T. H. Fritts field notes, 11 April 1970).

KU 138411–44 from 5 km NE La Unión, Región de Huánuco, Peru.—Juveniles have a yellowish-tan, grayish-beige, yellowish-green, or leaf-green dorsum; most are unicolor, but a few have brownish-bronze or yellowish-green blotches. In the smallest individuals (< 20 mm) the posterior surfaces of the thighs are tannish brown, with a few white flecks; the anterior surfaces of the thighs are yellowish tan. Larger juveniles (> 20 mm) have a prominent elongate orange blotch on the distal half of the posterior surface of the thigh, and another orange blotch in the axilla. The orange color becomes progressively fainter in subadults. In adults the dorsum is gray, beige, or tan with green, tan, or brown blotches on the body. The dorsal surfaces of the thighs are yellowish tan, with prominent bars corresponding to the color of the blotches on the body. The posterior surfaces of the thighs are brownish tan, with white or beige flecks; the anterior surfaces of the thighs are yellowish tan. The iris is metallic bronze (T. H. Fritts field notes, 15 March 1970).

KU 139189–90 from 10 km S Carhuamayo, Región de Junín, Peru.—The dorsum is tan, with dark brown blotches. The throat is creamy yellow; the belly is pale gray. The posterior surfaces of the thighs are pinkish tan. The iris is coppery bronze, with black reticulations (W. E. Duellman field notes, 26 January 1971).

MEASUREMENTS

Despite the large number of specimens available, only 21 adults were suitable for measurement (Table 12.18).

CRANIAL OSTEOLOGY

The sphenethmoid is smooth; the rest of the skull table is sculptured in a semicoarse pattern of shallow pits and low rounded ridges. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal does not articulate with the anterolateral margin of the frontoparietal. The frontoparietals lack a complete articulation medially, and have a narrow supraorbital flange; an otic flange is absent. A temporal arcade is absent. The frontoparietal covers only the anterior epiotic eminence; the carotid canal is open, and posteriorly exits the skull through the frontoparietal. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for about half the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is short. The maxilla lacks a distinct postorbital process; the slender zygomatic ramus of the squamosal articulates with the margin of the pars facialis of the

Table 12.18 Univariate statistics for adults of *Gastrotheca peruana*

	Males (n = 12)			Females (n = 9)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length*	43.7	33.6–52.6	6.65	48.2	40.7–56.5	4.87
Tibia length*	18.2	15.6–23.3	2.04	21.1	15.6–25.3	2.71
Foot length*	18.5	15.2–23.7	2.96	20.3	17.7–25.3	1.89
Head length*	14.1	10.6–17.1	2.74	15.6	12.0–18.3	2.26
Head width*	15.5	11.8–17.9	2.03	17.4	15.1–20.2	1.29
Interorbital distance*	3.7	3.1–4.6	0.51	4.5	3.6–5.1	0.40
Eyelid width	3.8	2.6–5.2	0.86	4.1	3.2–5.3	0.63
Internarial distance	2.6	1.6–3.4	0.79	2.5	1.7–3.5	0.61
Eye diameter	3.9	3.0–4.8	0.58	4.2	3.6–4.7	0.33
Eye–nostril distance	3.2	2.7–4.5	0.57	3.9	2.8–6.8	1.22
Orbit–jaw distance*	2.0	1.1–2.5	0.40	2.3	1.6–3.0	0.49
Nostril–jaw distance	3.2	2.3–3.9	0.48	3.4	2.6–4.0	0.42
Tympanum diameter	2.3	1.3–3.0	0.59	2.3	1.3–3.2	0.77
Thumb length*	7.4	5.8–9.1	0.95	8.4	6.6–9.7	1.18
Third finger length*	12.4	10.5–15.4	1.67	14.3	12.1–16.6	1.49

*Differences between the means of the sexes are significant ($P \leq 0.01$).

maxilla. The head of the squamosal has a narrow crest; the narrow otic plate articulates marginally with the crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in size, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows gradually anterior to the optic fenestra, and has a blunt terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are widely separated medially, and are smooth ventrally. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a broad triangular process on the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located between the posterior quadrants of the choanae.

Life History

No brooding females are available. At least throughout most of its range, *Gastrotheca peruana* produces eggs that hatch as tadpoles in Stage 31. Antonio W. Salas (pers. comm.) observed that at higher elevations in Región de Ancash, Peru, hatchling tadpoles are at more advanced stages. Pablo Chuna Mogollón (pers. comm.) observed that females at higher elevations (> 3000 m) in Región de La Libertad, Peru, produce eggs that hatch as froglets; at lower elevations (ca. 2300 m) the eggs hatch as tadpoles with no hind limbs, whereas at intermediate elevations they hatch as tadpoles with hind limbs. This apparent elevational gradient in the tadpoles' stage at hatching needs to be investigated more thoroughly. A strict elevational gradient is not supported by data from Región de Cajamarca (to the north of Región de La Libertad), where tadpoles have been collected at an elevation of 3520 m.

Tadpoles

A typical tadpole in Stage 37 (KU 215630) has a body length of 25.0 mm, and a total length of 62.0 mm. In dorsal view the body is elongately ovoid; the sides are nearly parallel along two-thirds the length of the body; the snout is bluntly rounded. In profile the body is highest posteriorly, gradually inclined to a rounded snout, and is wider than high. The throat is convex. The eyes are moderately small, and are directed dorsolaterally with an anterior inclination. The interorbital distance is about one-third the width of the body at the level of the orbits. The nostrils are slightly closer to the eyes than the tip of the snout. The spiracular tube is short, and is attached to the body throughout its length. The spiracular opening is directed posteriorly on the ventrolateral surface of the body at a point about 60% of the length of the body. The cloacal tube is short, conical, and dextral, with a diagonal opening. The caudal musculature is moderately robust, and is slightly higher than the dorsal fin at midlength of the tail. The musculature terminates in a pointed tip well within the margin of the caudal fin. The dorsal fin arises gradually from the proximal part of the caudal musculature. The dorsal and ventral fins are subequal in height at midlength of the tail, and terminate in a rounded tip.

The width of the oral disc is about one-third the width of the body. The disc is bordered laterally by a single row of short blunt marginal papillae, and ventrally by two rows of alternating papillae. There are two upper and three lower rows of labial teeth; the upper rows are slightly longer than the lower ones, and are subequal in length. The lower rows are progressively shorter; the second upper and first lower rows are narrowly interrupted medially. The upper jaw sheath is heavy, and is broadly arch-shaped; the lower sheath is massive, and is broadly V-shaped. Both sheaths bear numerous pointed serrations.

In preservative the body is dull brown. The skin on the posterior half of the lateral surfaces and on the venter is unpigmented. The caudal musculature is cream, with a brown streak along the upper edge. The fins are translucent, with fine brown reticulations on the dorsal fin. In life, the dorsum is greenish gray. The venter is grayish white. The largest individuals are green, with brown spots (W. E. Duellman field notes, 17 January 1989).

Tadpoles from throughout the range are alike structurally, but there is some variation in coloration in life, as evidenced from the following descriptions of living individuals.

KU 138771 from 5 km N Recuay, Región de Ancash, Peru.—The dorsum is pale grayish green, with a dark green canthal line grading to a grayish-green labial region. The venter is beige, with a metallic-green and bronze tint. The caudal musculature is pale grayish green; the fins are translucent, with occasional grayish-green flecks (T. H. Fritts field notes, 11 April 1970).

KU 138772 from 5 km NE La Unión, Región de Huánuco, Peru.—The largest individuals have a grayish-green dorsum; some have faint yellowish-green blotches. There is an irregularly defined grayish-green line along the caudal musculature; the translucent caudal fin has numerous gray-green flecks. The venter is transparent, with a bronze tint. Smaller individuals have a grayish-green dorsum, with extensive blackish-green flecking; the caudal musculature and fins have some blackish-green reticulations (T. H. Fritts field notes, 15 March 1970).

Advertisement Call

The call consists of a low-pitched "wraaack," usually followed by two or three shorter notes.

Distribution and Ecology

Gastrotheca peruana is known from elevations of 4000–4600 m in the northern headwaters of the Río Mantaro on the southern slope of the Nudo de Pasco in central Peru, elevations of 2300–3350 m in the upper valley of the Río Marañón, and elevations of 2300–3520 m on the Pacific slopes of the Cordillera Occidental in the northern half of Peru (Fig. 12.38). Most individuals have been found under rocks in supratreeline grassland, but a few have been observed on low vegetation (< 30 cm) at the edges of ponds. Tadpoles have been found in shallow grassy pools and marshes.

Conservation Status

This species is categorized as being of Least Concern in the IUCN Red List. It may be endangered in several extensive mineral concessions throughout its range (Aguilar et al., 2012).

Etymology

Although Boulenger (1900) did not so state, the specific name *peruana* refers to the country of origin of the type specimens.

Remarks

Three subspecies of *Gastrotheca peruana* were recognized by Vellard (1957), who distinguished the populations as follows.

G. p. peruana. Head width about equal to head length; feet relatively large; dorsal glands (pustules) well developed (Cordillera Occidental from Cajamarca to Anash).

G. p. dissimilis. Head wider than long; feet relatively large; dorsal pustules not so well developed (cordilleras in Cajamarca).

G. p. junensis. Head wider than long; feet short; dorsal pustules well developed (highlands of Huánuco, Junín, and Pasco).

Based on their observations on coloration, Duellman and Fritts (1972:15) stated: "Until the nature of the changes [ontogenetic in coloration] and the geographical limits of various populations are known, it is not feasible to recognize subspecies of *G. peruana*." In order to evaluate the geographic variation in this species more critically, data on specimens from four geographic regions were subjected to multivariate analyses: Cajamarca ($n = 10$), corresponding to *G. p. dissimilis*; Ancash ($n = 11$), corresponding to *G. p. peruana*; and Huánuco ($n = 13$) and Junín ($n = 2$), corresponding to *G. p. junensis*. Morphometric data were analyzed using a stepwise discriminant functions analysis (Fig. 12.39). In a jackknifed five-step model of $\log_{10}$ data, only 56% of the specimens were classified correctly as to population. In Figure 12.39, the variables that entered the model on the first axis indicate that snout–vent

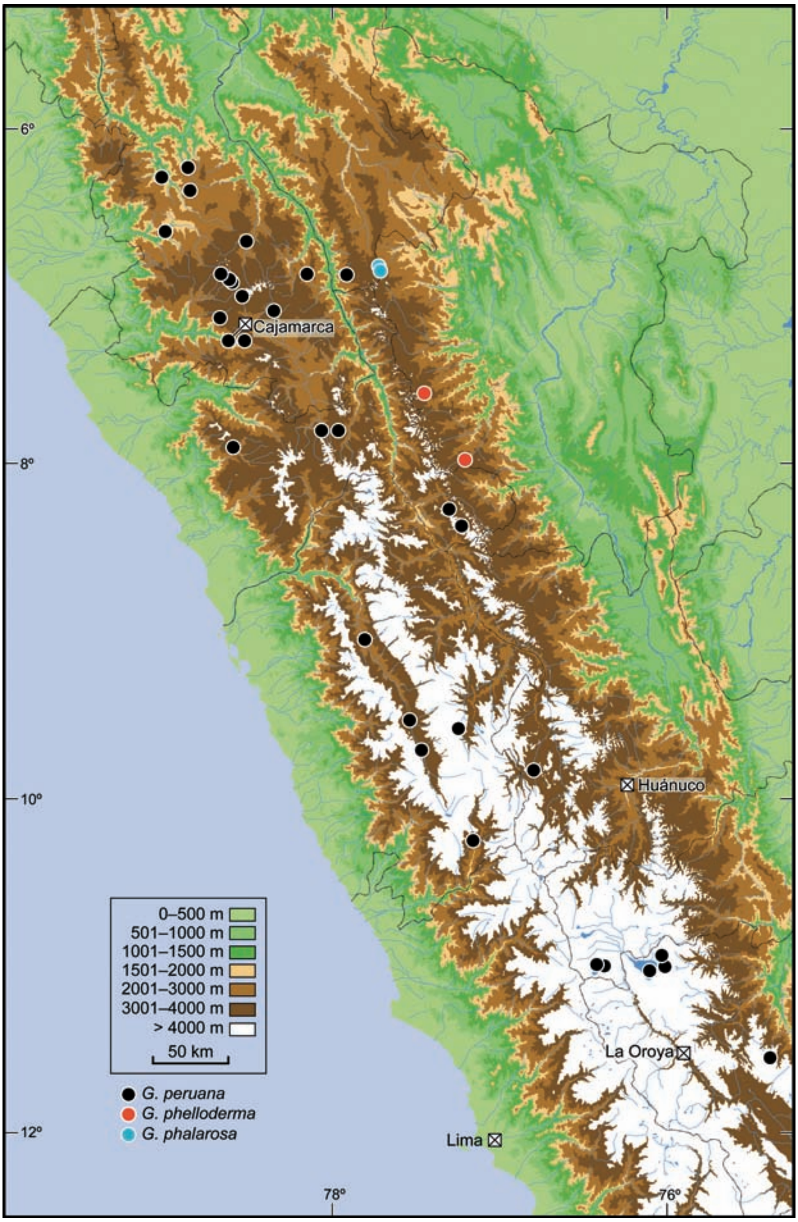
6°
8°
10°
12°
78°
76°
Cajamarca
Huánuco
La Oroya
Lima
0–500 m
501–1000 m
1001–1500 m
1501–2000 m
2001–3000 m
3001–4000 m
> 4000 m
50 km
G. peruana
G. phelloderma
G. phalarosa

Fig. 12.38 Andean region of northern and central Peru, showing the localities of known occurrences of *Gastrotheca peruana*, *phelloderma*, and *phalarosa*.

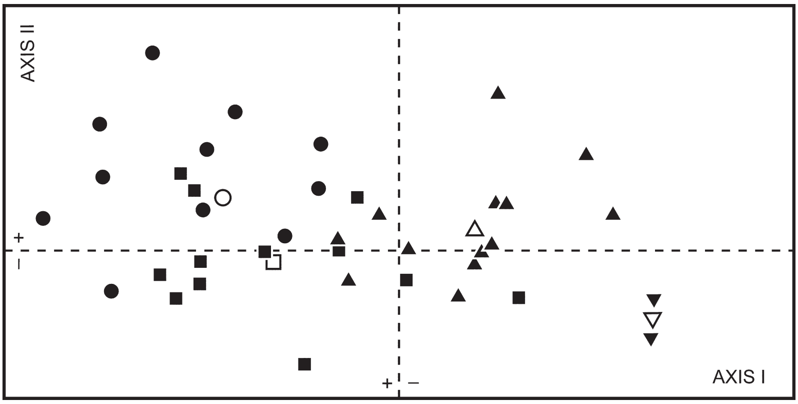

Fig. 12.39 Multivariate plot of a stepwise discriminant analysis of morphometrics of four populations of *Gastrotheca peruana* in northern and central Peru. Circles = from Departamento Cajamarca; squares = from Departamento Ancash; triangles = from Departamento Huánuco; inverted triangles = from Departamento Junín. Open symbols = means of the samples.

length, head width, and eyelid width are greater in specimens from Cajamarca and Ancash that in those from Huánuco and Junín, whereas on the second axis thumb length and eye diameter are incorporated. Thus the different populations cannot be discriminated effectively by size factors, but there does seem to be a trend in decreasing snout–vent length from north (Cajamarca) to south (Junín).

The pustularity of the skin on the dorsum varies from large elevated pustules to ones that are barely evident. Much of this variation in preserved specimens depends on their state of preservation: specimens that are soft tend to have smoother skin that those that were preserved in stronger formalin. Furthermore, the least pustular individuals in life that I have examined are from Junín, the region in which the pustularity is strongest, according to Vellard (1957). In other structural characters, especially the amount of webbing, specimens from throughout the range are remarkably uniform.

Geographic variation in color pattern was analyzed in five populations by a cluster analysis, which grouped individuals on the basis of six variable characters (Fig. 12.40). In this analysis, specimens from Ancash fell out in six of the nine branches, and those from Huánuco fell out on eight branches. Of the 47 specimens, 24 (51%)—representing all five populations—are on one branch, on which the frogs are characterized by uniformly pale posterior surfaces of the thighs, no flecks on the venter, a patterned dorsum, and a labial stripe. The foregoing analyses provide no data to support the recognition of more than one taxon. Thus subspecies are not recognized in *G. peruana*. Molecular data are likely to reveal cryptic species, for which some of Vellard's names may be applicable.

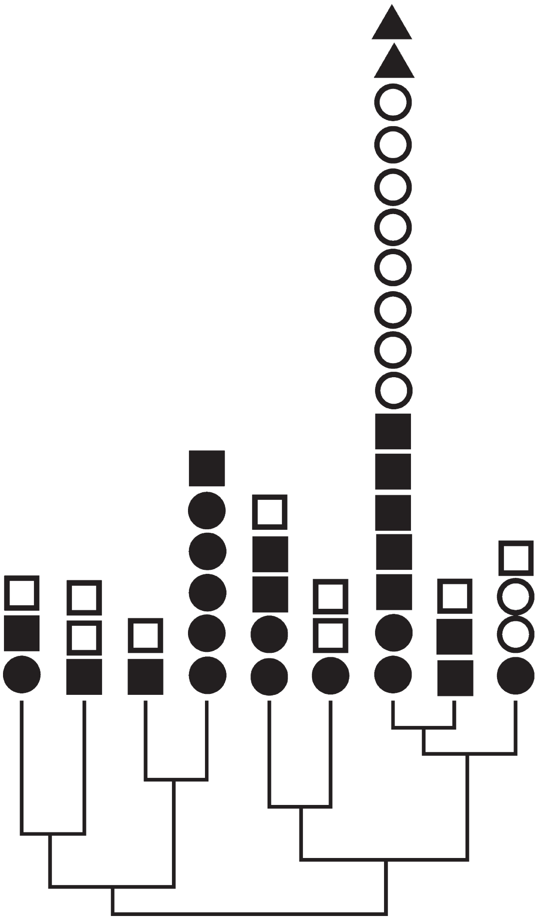

Fig. 12.40 Phenogram, based on a cluster analysis of the color patterns in *Gastrotheca peruana* from five departments throughout its range. Each symbol represents one individual. Solid circles = from Ancash, open circles = from Cajamarca, solid squares = from Huánuco, open squares = from La Libertad, solid triangles = from Junín.

Gastrotheca (Gastrotheca) phalarosa Duellman and Venegas

Gastrotheca phalarosa Duellman and Venegas, 2005:299.—Holotype: MUSM 19487, an adult male, from Esperanza, 3435 m, Provincia de Huallaga, Región de San Martín, Peru.

Diagnosis

This medium-sized species attains a maximum known snout–vent length of 45.2 mm. The tibia length is less than 50% of the snout–vent length, and is shorter than the foot. The interorbital distance is slightly greater than the width of the upper eyelid. The skin on the dorsum is smooth with scattered prominent pustules, not co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is longer than the second; the discs on the fingers are barely wider than the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends maximally to a point proximal to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is grayish tan, with black paravertebral marks. Markings on the head consist of a narrow white canthal stripe and white spots on the lips. A pale dorsolateral stripe is absent. The flanks and venter are black, with white spots.

Among other short-legged Andean species of *Gastrotheca* in which the skin is not co-ossified with the underlying cranial elements, only two (*G. espeletia* and *G. ruizi*) are like *G. phalarosa* in having the first finger longer than the second. Both of these species are like *G. phalarosa* in having inclined protruding snouts in profile, fingers with discs barely wider than the adjacent segments of the digits, and interorbital distances equal to or only slightly greater than the width of the upper eyelid. They differ from *G. phalarosa* by having smooth skin, without pustules on the dorsum. Furthermore, the venter is uniformly dark gray in *G. ruizi* and cream with dark gray flecks or weak mottling in *G. espeletia*, in contrast to the black venter with white spots in *G. phalarosa*. The latter is like *G. peruana* in having an inclined protruding snout in profile, interorbital distance about equal to the width of the upper eyelid, and pustular skin on the dorsum. *G. phalarosa* differs from *G. peruana* (conditions of the latter in parentheses) by having a nearly truncate snout in dorsal view (acutely rounded), nostrils posterior to the level of the anterior margin of the lower jaw (at level of anterior margin of lower jaw), tympanic annulus that is barely evident and smooth (annulus distinct and granular), inner tarsal fold that is evident only distally (extending full length of tarsus), and in coloration: narrow white canthal stripe (broad black stripe), no pale labial stripe (stripe present), and black venter with white spots (tan venter with or without brown flecks).

Description

The following description is based on two adult males. The body is robust; the maximum known snout–vent length is 45.2 mm in males. The head is wider than long, but not as wide as the body. The snout is nearly truncate in dorsal view, and in profile is convexly inclined anteroventrally and protruding. The canthus rostralis is slightly curved, rounded in cross-section, and not elevated. The loreal region is noticeably concave; the lips are rounded. The top of the head is flat. The interorbital distance is slightly greater than the width of the upper eyelid. The internarial area is slightly depressed. The nostrils are barely protuberant, and are directed laterally with a slight anterior inclination at a level well posterior to the anterior margin of the lower jaw. The diameter of the eye is equal to its distance from the nostril. The tympanum is nearly round, and is separated from the eye by a distance greater than the diameter of the tympanum. The tympanic annulus is smooth, and is barely evident. The supratympanic fold is weak and rounded above the tympanum, but is enlarged (almost globular) posteroventrally and obscures the posterior edge of the tympanum.

The arm is moderately robust, and lacks ulnar tubercles. The hand is moderately large. The fingers are moderately long, and bear small terminal discs; the width of the disc on the third finger is about two-thirds the diameter of the tympanum. The relative lengths of the fingers are I > I < IV < III. The fingers are unwebbed, but bear narrow fleshy lateral fringes. The subarticular tubercles are moderately large and subconical; the supernumerary tubercles are small, subconical, and present only on the proximal segments of the third and fourth fingers. There is no palmar tubercle; the prepollical tubercle is low, wide, and diffuse proximally, and is bluntly elliptical distally; nuptial excrescenses are absent. The hind limb is short, and is moderately robust. The tibia length is about 43% of the snout–vent length; the foot length is about 46% of the snout–vent length. The heel lacks a calcar or tubercle. An outer tarsal fold and tarsal tubercles are absent; the inner tarsal fold is barely evident on the distal one-fifth of the tarsus. The inner metatarsal tubercle is elevated, ovoid, and visible from above; an outer metatarsal tubercle is absent. The toes are long and slender, and have fleshy lateral fringes and small terminal discs that are no wider than the adjacent phalangeal segments. The relative lengths of the toes are I < II < III = V < IV. The outer toes are about one-fifth webbed; the webbing formula is **I**2—3^+**II**2^+—3^+**III**3^-—4**IV**4—2**V**. The subarticular tubercles are low and rounded; the supernumerary tubercles are low, rounded, and present only on the proximal segments of Toes II–IV.

The skin on the dorsal surfaces of the head, body, and limbs is smooth, with scattered small pustules on the upper eyelids and large and small pustules on the body; the skin on the flanks is shagreen; the skin on the venter is smooth; the skin on the posterior part of the belly and proximal posteroventral surfaces of the thighs is granular. Supraciliary processes and transverse dermal ridges are absent. Enlarged paracloacal tubercles are absent. The dentigerous processes of the vomers are transverse, and are narrowly separated medially between the ovoid choanae. Each process bears zero to three teeth.

COLOR IN PRESERVATIVE

The dorsal surfaces of the head, body, and limbs are grayish tan, with black markings narrowly outlined with white. These consist of an ovoid spot on each upper eyelid, broad paravertebral markings from the occipital region to the upper inguinal region that are narrowly connected posteriorly to a narrowly triangular median postsacral mark with the apex positioned anteriorly, broad transverse marks on each thigh and shank, and an irregular transverse mark on each fore-

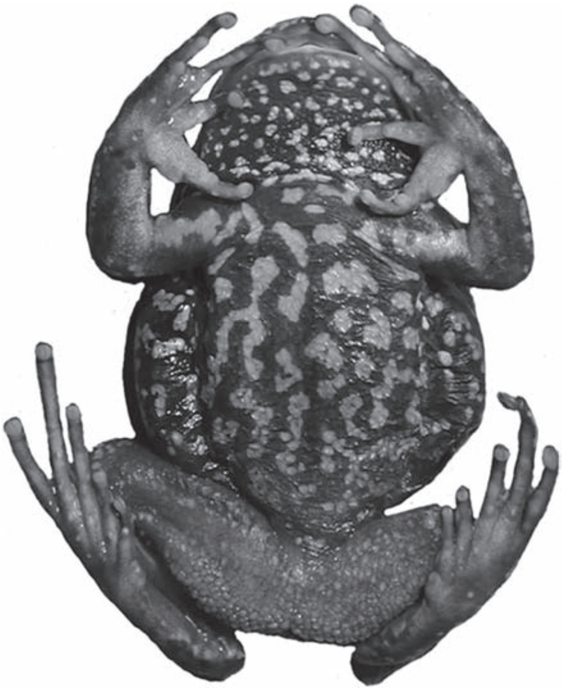

Fig. 12.41 Ventral color pattern of *Gastrotheca phalarosa* (MUSM 19487, holotype), male, 43.3 mm SVL, Esperanza, 3435 m, San Martín, Peru. Photo by W. E. Duellman.

arm. Other dorsal surfaces of the limbs, including the hands, feet, and digits, are black with small irregular white spots. Small irregular black marks are present middorsally on the head and body. The flanks are black, with white spots or mottling. A narrow white canthal stripe borders the black loreal region. The labial and tympanic regions are black, with irregular white dashes and small spots. The anterior surfaces of the thighs are black; each has two narrow vertically transverse white lines and a few small black spots. The posterior surfaces of the thighs are black; tubercles ventrolateral to the cloacal opening are tipped with white. The throat and belly are black, with white spots that are smaller on the throat than on the belly (Fig. 12.41). The palmar and plantar surfaces are grayish tan; the other ventral surfaces are black, with irregular white markings. The lower eyelid is gray, with a black edge. The iris is mottled gray and white.

COLOR IN LIFE

The dorsum is creamy tan to reddish, with dark brown markings that correspond to the dark markings visible in preservative (Fig. 12.42). Metallic-green flecks and short stripes are evident on the dorsum. The transverse marks on the limbs are green, with narrow black borders. The flanks are mottled black and white. The venter is black, with creamy white spots. The iris is reddish bronze or pale bronze, with reddish-brown flecks.

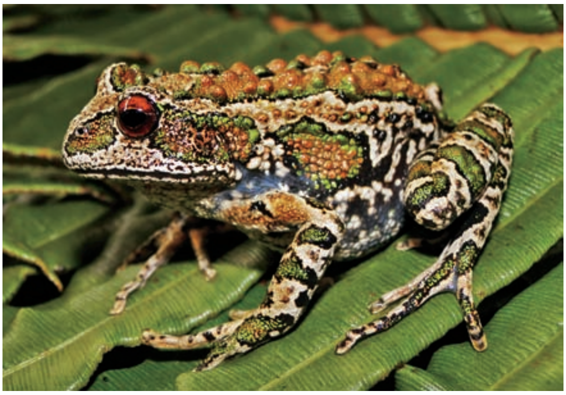

Fig. 12.42 *Gastrotheca phalarosa* (CORBIDI 11044), female, Quintecocha, 3135 m, San Martín, Peru. Photo by P. Venegas, KUDA.

Table 12.19 Measurements (in mm) for two adult male *Gastrotheca phalarosa* specimens

Character	MUSM 19487	MUSM 19472
Snout–vent length	43.3	45.2
Tibia length	18.5	19.5
Foot length	15.5	21.3
Head length	15.7	15.0
Head width	16.4	17.8
Interorbital distance	4.3	5.0
Eyelid width	4.0	4.2
Internarial distance	4.0	3.5
Eye diameter	4.3	4.5
Eye–nostril distance	4.3	4.1
Orbit–jaw distance	2.5	2.8
Nostril–jaw distance	3.5	3.7
Tympanum diameter	2.2	3.1
Thumb length	7.8	8.2
Third finger length	13.4	11.3
Disc width	1.5	1.4

MEASUREMENTS

The measurements of the two known males are given in Table 12.19.

CRANIAL OSTEOLOGY

Some aspects of the cranial osteology can be ascertained from radiographs of MUSM 19487. The dermal roofing bones are not co-ossified with the overlying skin; the dermal sphenethmoid is weakly sculptured. The nasals weakly articulate medially; their borders are distinct from the sphenethmoid. The frontoparietals have an incomplete articulation medially, and each has a narrow supraorbital flange. A temporal arcade is absent. The otic and zygomatic rami of the squamosal are narrow; the zygomatic ramus appears to articulate with the maxilla.

Life History

Several tadpoles found at the type locality on 18 November 2003 in a small pool, with a depth of 40 cm and a mud substrate, were feeding on a dead earthworm. Some of these tadpoles were raised in captivity; they metamorphosed into *Gastrotheca phalarosa*.

Tadpoles

A tadpole in Stage 39 (MUSM 19498) has a body length of 29.4 mm, and a total length of 65.5 mm. In dorsal view, the body is ovoid, blunt posteriorly, and abruptly narrowing to a rounded snout anterior to the orbits. There are no lateral indentations. The body is highest at a point slightly anterior to midlength, gradually diminishes in height to the level of the orbits, and then abruptly decreases in height from the level of the nares to the snout. The throat is slightly concave. The eyes are small, situated more dorsally than laterally, and slightly inclined anterolaterally. The interorbital distance is more than twice the diameter of the eye. The nares are large, have a low rim, and are situated about midway between the tip of the snout and the orbits. The spiracular tube is sinistral, curved posterodorsally, and is attached to the body throughout its length. The spiracular opening is directed dorsolaterally well below midline of the body. The cloacal tube is dextral, elongately cone-shaped with a transverse aperture, and is attached throughout its length to the ventral fin. The caudal musculature is massive, and gradually tapers to a point well within the margin of the caudal fins. The dorsal fin originates on the base of the caudal musculature, increases in height on the proximal one-fourth of the tail, maintains an equal height throughout the middle half of the tail, and gradually diminishes to a rounded tip. The ventral fin originates on the body wall, and is highest at about one-third the length of the tail. At midlength of the tail the height of the dorsal fin is about half that of the caudal musculature; the height of the ventral fin is about one-fourth the height of the caudal musculature.

The oral disc is directed more anteriorly than ventrally; its width is about one-third the greatest width of the body. There is a single row of large conical marginal papillae laterally and ventrally, with these papillae largest laterally; there are five to seven small submarginal papillae ventrolaterally. There are two upper and three lower rows of labial teeth; the rows extend laterally to the marginal papillae. The teeth are long and slender; those on the third lower row are smaller than the others. The jaw sheaths are moderately massive, and are finely serrate. The upper sheath is broadly arch-shaped; the lower sheath is broadly V-shaped.

In life and in preservative, the tadpoles are black dorsally and ventrally. The viscera are not visible through the ventral body wall. The caudal musculature is black; the caudal fins are translucent gray.

Advertisement Call

No data are available.

Distribution and Ecology

Gastrotheca phalarosa is known only from two localities, at elevations of 3119 and 3435 m in the northern part of the Cordillera Central in northern Peru (Fig. 12.38). At the type locality, the frogs were found by day in areas of bunchgrass and scattered bushes (*Baccharis*), shrubs, and spiny bromeliads.

Conservation Status

This species is categorized as Data Deficient in the IUCN Red List.

Etymology

According to Duellman and Venegas (2005), the specific name is a Greek adjective, *phalaros*, meaning "white-spotted"; the name refers to the distinctive ventral coloration.

Remarks

The general habitus of this species and the features of the skull that can be determined suggest that it may be related to *Gastrotheca peruana*, but genomic data do not place it as a sister species of that taxon.

Gastrotheca (*Gastrotheca*) *phelloderma* Lehr and Catenazzi

Gastrotheca phelloderma Lehr and Catenazzi, 2011:450.
Holotype: MUSM 27739, an adult female, from Pampa del Cuy, Parque Nacional del Río Abiseo, ± 24 km NE Pataz, 3400 m, Provincia de Mariscal Cacerés, Región de San Martín, Peru.

Diagnosis

Adults of this medium-sized species attain a maximum snout–vent length of 57.7 mm. The tibia length is less than 52% of the snout–vent length, and is slightly shorter than the foot. The interorbital distance is slightly less to slightly greater (71%–141%) than the width of the upper eyelid. The skin on the dorsum is smooth, has prominent longitudinal pustular ridges, is not co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is slightly longer than the second; the fingers bear discs that are about the same width as the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends to the penultimate subarticular tubercle on the fourth toe and the distal subarticular tubercle on the fifth toe. The dorsum is pale grayish brown, with reddish-brown paravertebral markings. Markings on the head consist solely of a pale margin on the upper lip. Pale dorsolateral stripes are absent. The flanks are tan, with a reddish-brown diagonal mark extending from a point behind the jaw to midflank. The venter is cream.

Gastrotheca phelloderma has distinctly elevated angular canthal ridges; similar ridges exist in *G. galeata*, but it differs from *G. phelloderma* by having a spatulate head with flared maxillae and premaxillae, extensive dermal-cranial co-ossification, and an elevated transverse occipital ridge. Dark brown pustular longitudinal paravertebral ridges also occur in some *G. peruana*, which differs from *G. phelloderma* by having Fingers I and II equal in length and a granular tympanic annulus, whereas the annulus is smooth in *G. phelloderma*. Paravertebral dark brown markings similar to those in *G. phelloderma* also occur in several other species (e.g., *G. lateonota* and *G. monticola*) in northern Peru and southern Ecuador. All of these differ from *G. phelloderma* by having Fingers I and II equal in length or Finger I shorter than Finger II. as opposed to Finger I being longer than Finger II in *G. phelloderma*. Also, in those species the discs on the fingers are wider than the digits proximal to the discs, whereas they are about the same width in *G. phelloderma*. In addition, *G. monticola* differs from *G. phelloderma* by having small irregular black spots on a cream venter; the venter is uniformly cream in *G. phelloderma*. Two other species of *Gastrotheca* are known from the northern part of the Cordillera Central in Región de San Martín. Of these, *G. ossilaginis* has the skin on the dorsal surface of the skull co-ossified with the underlying dermal bones, and has shagreen skin on the dorsum, with no pustular longitudinal ridges. *G. phalarosa* differs by having a black venter with white spots, no longitudinal ridges, and a weak tarsal fold distally, whereas the tarsal fold is well developed along the length of the tarsus in *G. phelloderma*.

Description

The following description is based on 31 specimens. The body is moderately robust. The maximum snout–vent length is 43.8 mm in males, and 53.5 mm in females. The head is wider than long, but not as wide as the body. The snout is rounded in dorsal view, and is bluntly rounded in profile. The canthus rostralis is elevated, straight, and angular in cross-section. The loreal region is concave; the lips are slightly flared. The top of the head is flat to slightly depressed. The interorbital distance is 71%–141% of the width of the upper eyelid. The internarial area is slightly concave. The nostrils are barely protuberant laterally, and are directed anterolaterally at a level posterior to the level of the anterior margin of the lower jaw. The diameter of the eye is greater than its distance from the nostril. The tympanum is vertically ovoid, and is separated from the eye by a distance about equal to the diameter of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately weak, extending from the posterior corner of the orbit, curving ventrally posterior to the tympanum, and barely covering the posterior edge of the tympanum.

The arm is moderately robust and long; ulnar tubercles are absent. The hand is large. The fingers are long, unwebbed, and bear distinct narrow lateral keels. The discs on the fingers are small, and are about equal in width to the digits proximal to the discs. The width of the disc on Finger III is about half the diameter of the tympanum. The relative lengths of the fingers are I > II < IV < III. The subarticular tubercles are moderately large, round, and conical in profile; none are bifid, except for those on Finger I in some specimens. The supernumerary tubercles are numerous, moderately large, and subconical. The palmar tubercle is low and bifid; the prepollical tubercle is elliptical; males have pale cream nuptial excrescences on the dorsal surfaces of the thumbs. The hind limb is moderately robust. The tibia length is 39%–52% of the snout–vent length; the foot length is 38%–53% of the snout–vent length. The heel lacks a calcar or tubercle. The outer tarsal fold is distinct and slightly undulated, extending nearly the entire length of the tarsus. The inner metatarsal tubercle is ovoid and subconical; an outer metatarsal tubercle is absent. The toes are long, with distinct narrow lateral keels. The terminal discs are round, and are about equal in width to the digits proximal to them. The relative lengths of the toes are I < II < III < V < IV. The toes are about one-third webbed; the webbing formula is **I**2—3**II**2—3**III**2—2**IV**2—2**V**. The subarticular tubercles are moderately large, ovoid, and conical in profile; the penultimate subarticular tubercle on Toe

IV is weakly bifid in some individuals. The supernumerary tubercles are small, numerous, and subconical.

The skin on the dorsum of the head, body, and limbs is smooth, with prominent longitudinal pustular ridges and many scattered pustules; the skin on the flanks is tubercular; the skin on the throat, belly, and anteroventral surfaces of the thighs is granular; the skin on the posteroventral and posterior surface of the thighs has small conical tubercles; the other surfaces are smooth. Large pustules are present on the inner margin of the upper eyelid; small elevated pustules are present on the dorsal surface of the head. Prominent paravertebral ridges of elongate coalesced warts continue from the scapular region to the level of the sacrum; in females, two additional ridges extend from the opening of the brood pouch to the level of the groin. An irregular dorsolateral fold is formed by narrowly separated ovoid warts extending from the level of the insertion of the arm to the groin. Three moderately large tubercles are present ventrolateral to the cloacal opening. The opening of the brood pouch is narrowly U-shaped, with the anterior border at the level of the posterior edge of the sacrum. The dentigerous processes of the vomers are narrowly separated medially between small ovoid choanae. Each process bears four to five teeth.

COLOR IN PRESERVATIVE

The dorsum and flanks are dark gray. A dark grayish-brown blotch is evident on the upper eyelid in most specimens; an interorbital bar is absent. Prominent dark grayish-brown irregularly shaped paravertebral marks are either continuous or narrowly interrupted, and extend from the occiput to the postsacral area. The dorsal surfaces of the limbs are gray, with darker grayish-brown blotches. The sides of the head are dark gray. A canthal stripe is absent; the upper lip is pale gray below the eye; the tympanum is pale gray. An irregularly shaped dark grayish-brown postorbital stripe extends from the posterior corner of the orbit, across the upper part of the tympanum, to the middle of the flank that otherwise is gray, with minute black flecks. The chest, belly, and ventral surfaces of the limbs are cream; the plantar surfaces are pale gray. In females the throat is pale gray to white, with a few black spots marginally; in males the vocal sac is cream, with dark gray or brown flecks.

COLOR IN LIFE

The following description is based on color notes and photos taken by Alessandro Catenazzi. A color photo of MUSM 15965 (Fig. 12.43), an adult male, reveals a yellowish-tan middorsal stripe, with broader reddish-brown paravertebral marks extending from the eyelids to the postsacral region, where the marks converge. A narrow tan canthal stripe extends across the outer edge of the upper eyelid, and expands in width as it continues to the groin. The canthal region, postorbital area, and upper flanks (to the level of the sacral region) are dull brown. The lips are pale gray. The lower flanks and inguinal region are grayish tan, with black flecks. The limbs are yellowish tan, with reddish-brown transverse bars. The iris is reddish brown, with black reticulations and a bronze ring around the pupil. According to Catenazzi's field notes, the venter is cream, with a pattern of brown spots; palmar and plantar surfaces and the perianal region are yellow. Catenazzi described the male (MUSM 15965) as having a grayish-tan dorsum, with reddish-brown paravertebral marks that extend from the upper eyelid to the cloacal opening and are bordered by pale gray. The upper lip is grayish tan, with a pale gray to white mark from below the eye to the tympanum. Reddish-brown flecks are present on the side of the head posterior to the eye; a reddish-brown stripe bordered by black extends from the tympanum to the middle of the flank. The flank is grayish tan, with a few minute dark brown spots. A few pale green flecks are present on the top of the head. The dorsal surfaces of the limbs are pale gray, with reddish-brown ovoid blotches bordered by dark brown. The venter is pale gray.

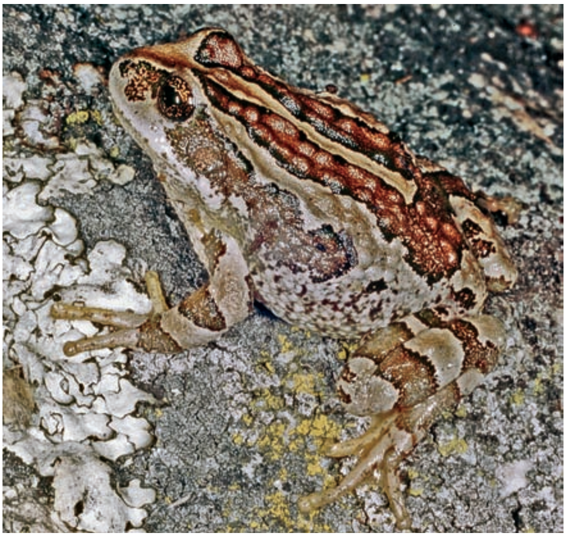

Fig. 12.43 *Gastrotheca phelloderma* (MUSM 15965), male, 42.0 mm SVL, Parque Nacional del Río Abiseo, San Martín, Peru. Photo by A. Catenazzi, KUDA.

Table 12.20 Univariate statistics for adults of *Gastrotheca phelloderma* (from Lehr and Catenazzi, 2011)

	Males ($n = 6$)			Females ($n = 21$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	41.6	35.3–43.8	3.2	53.5	46.9–57.7	3.0
Tibia length	19.4	18.4–20.4	0.9	23.6	21.8–27.0	1.4
Foot length	19.8	18.7–21.1	0.9	24.1	21.2–26.6	1.3
Head length	16.7	16.1–18.1	0.7	19.5	18.0–21.4	1.0
Head width	18.1	16.2–19.5	1.2	21.4	19.1–3.3	0.9
Interorbital distance	4.4	3.3–5.3	0.6	5.4	3.4–6.6	1.0
Eyelid width	4.3	3.7–4.9	0.4	5.0	3.9–6.2	0.6
Internarial distance	3.1	2.9–3.3	0.2	3.6	3.1–4.1	0.3
Eye diameter	4.6	4.3–4.8	0.2	5.4	4.6–6.2	0.4
Eye–nostril distance	4.6	3.7–5.2	0.5	5.0	4.5–5.7	0.3
Orbit–jaw distance	2.4	2.2–2.5	0.1	3.0	2.5–3.6	0.3
Nostril–jaw distance	3.4	2.2–3.6	0.2	4.1	3.7–5.1	0.3
Tympanum diameter	2.3	2.0–2.7	0.3	2.7	2.1–4.4	0.5
Thumb length	7.9	6.8–8.7	0.9	9.9	8.1–10.9	0.7
Third finger length	11.9	10.7–13.1	0.9	14.6	13.4–16.3	0.7
Disc width	1.5	1.3–1.6	0.1	2.0	1.5–2.3	0.2

MEASUREMENTS

Females are notably larger than males (Table 12.20).

CRANIAL OSTEOLOGY

No data are available.

Life History

Gastrotheca phelloderma produces eggs that hatch as tadpoles in the brood pouch. One female (KU 331038), having a snout–vent length of 57.5 mm, contained 45 eggs. Lehr and Catenazzi (2011) reported that two juveniles (MUSM 27606, Stage 46, snout–vent length 25.0 mm; MUSM 27754, Stage 45, snout–vent length 23 mm) have the typical coloration pattern, consisting of brown paravertebral marks extending from the upper eyelid to the sacrum, but their pustular longitudinal dorsal ridges are either weakly developed (MUSM 27606) or absent (MUSM 27754).

Distribution and Ecology

Gastrotheca phelloderma is known from only three localities, at elevations of 3308–3400 m on the Amazonian slopes and near the crest of the northern part of the Cordillera Central in northern Peru (Fig. 12.38).

Conservation Status

This species has not been categorized in the IUCN Red List. Lehr and Catenazzi (2011) noted that the conservation status of populations within Río Abiseo National Park is unknown. The fungus *Batrachochytrium dendrobatidis*, which causes chytridiomycosis in amphibians, has been detected in specimens of *Atelopus patazensis* near Río Abiseo National Park; this is a potential threat to *Gastrotheca phelloderma* in the park.

Etymology

According to Lehr and Catenazzi (2011), the specific name is derived from the Greek *phellos*, meaning "cork" or "bark," and the Greek *derma*, meaning "skin." The name alludes to the rough bark-like texture of the dorsal skin.

Remarks

Pablo Venegas (pers. comm.) has found numerous half-grown specimens, all of which are green dorsally.

Gastrotheca (*Gastrotheca*) *piperata* Duellman and Köhler

Gastrotheca piperata Duellman and Köhler, 2005:2.—Holotype: ZFMK 66838 from Sehuecas, Departamento de Cochabamba, Bolivia.

Diagnosis

In this moderately small species of *Gastrotheca* (females to 46.8 mm), the tibia length is about 49% of the snout–vent length, and is barely longer than the foot. The interorbital distance is about equal to the width of the upper eyelid. The skin on the dorsum is smooth to finely tuberculate, not co-ossified with skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is either smooth or granular. The first finger is shorter than the second; the discs on the fingers are only slightly wider than the digits. The fingers are unwebbed; on the foot the webbing extends maximally to a point midway between the preantepenultimate and antepenultimate subarticular tubercles on the fourth toe and a point midway between the antepenultimate and penultimate subarticular tubercles on the fifth toe. The dorsum is greenish, silvery, or golden tan, with black flecks. Markings on the head consist of a diffuse pale labial stripe and a narrow dark canthal stripe. A pale dorsolateral stripe is absent. The flanks are pale, with dark flecks; the venter is cream, with or without diffuse dark flecks.

Gastrotheca piperata is like several other species in the Andes of southern Peru, Bolivia, and Argentina in having a snout–vent length less than 55 mm, skin not co-ossified with the skull, no webbing between the outer fingers, no calcars or tubercles on the heels, the first finger shorter than the second, and no pale dorsolateral stripe. Among these species, *G. caeruleomaculata*, *christiani*, *chrysosticta*, *ochoai*, and *rebeccae* have proportionately much wider discs on the fingers than *G. piperata*, in which the discs are only slightly wider than the distal ends of the penultimate segments of the digits. Furthermore, the interorbital distance is at least nearly half again the width of the upper eyelid in *G. christiani*, *chrysosticta*, *excubitor*, *ochoai*, *pacchamama*, and *rebeccae*, in contrast to being about equal to the width of the upper eyelid in *G. piperata*. By usually lacking an interorbital bar and having a dorsal color pattern consisting of small black flecks, *G. piperata* differs from *G. gracilis* and *G. marsupiata*, in which the dorsal pattern consists of an interorbital bar and dark spots (usually in paravertebral rows) or middorsal and paravertebral dark marks.

Description

The following description is based on 24 specimens. The body is moderately robust; the maximum snout–vent length is 36.3 mm in males, and 46.8 mm in females. The head is slightly wider than long, and about as wide as the body. The snout is bluntly rounded in dorsal view and in profile. The canthus rostralis is acutely rounded in cross-section. The loreal region is concave; the lips are slightly flared and rounded. The top of the head is flat. The mean interorbital distance is 117% of the width of the upper eyelid. The internarial area is flat. The nostrils are slightly protuberant, and are directed anterolaterally at the level of the anterior margin of the lower jaw and below the anterior terminus of the canthus rostralis. The diameter of the eye is slightly greater than its distance from the nostril. The tympanum is round, and is separated from the eye by a distance equal to half again the length of the tympanum. The tympanic annulus is distinct, and is smooth or granular. The supratympanic fold is moderately heavy and tuberculate, extends from the posterior corner of the orbit to a point above the insertion of the arm, and obscures the upper and posterodorsal parts of the tympanum.

The arm is moderately robust, and lacks ulnar tubercles. The hand is moderately large. The fingers are unwebbed. The discs on the fingers are moderately small and round; the width of the disc on the third finger is about equal to the diameter of the tympanum. The relative lengths of the fingers are I < II < IV < III. The subarticular tubercles are large and subconical; none are bifid. The supernumerary tubercles are moderately large and subconical, and are numerous on the proximal segments. The palmar tubercle is large and weakly bifid; the prepollical tubercle is elongate and ovoid; nuptial excrescences are not evident. The hind limb is moderately slender. The tibia length is about 49% of the snout–vent length; the foot length is about 48% of the snout–vent length. The heel lacks a calcar or tubercle. The inner tarsal fold is distinct throughout the length of the tarsus. The outer metatarsal tubercle is small and round; the inner metatarsal tubercle is elevated, elongate, and visible from above. The toes are rather long. The relative lengths of the toes are I < II < III < V < IV. The toes are less than one-fourth webbed; the webbing formula is **I**2–2^{+}**II**2–3^{+}**III**3^{+}–3^{+}**IV**3^{+}–2^{+}**V**. The subarticular tubercles are subconical, and are smaller than those on the fingers. The supernumerary tubercles are minute, subconical, and present only on the proximal segments.

The skin on all dorsal surfaces is smooth, with small tubercles scattered on the head and upper eyelids; larger tubercles are present on the supratympanic fold and the side of the head posterior to the eye. The skin on the flanks, belly, and proximal posteroventral surfaces of the thighs is granular; cloacal tubercles and folds are absent. The opening of the brood pouch is narrowly U-shaped, with the anterior border posterior to the level of the sacrum. The dentigerous processes of the vomers are transverse at the level of the posterior margins of the small round choanae; the processes nearly abut medially. Each process bears four or five teeth.

COLOR IN PRESERVATIVE

The dorsum is dull gray, usually with scattered small dark brown to black flecks. Among 24 individuals, the dorsum is either uniformly grayish tan (12.5%) or is marked with dark flecks (58.3%), dark spots in three longitudinal rows (12.5%), dark flecks and dark spots in three longitudinal rows (8.3%), many small dark spots not arranged in longitudinal rows (4.2%), or dark reticulations (4.2%). The flanks are uniformly pale (25%) or marked with dark flecks (75%). The dorsal surfaces of the hind limbs are uniformly pale (12.5%), marked with dark flecks (79.3%), or have two narrow transverse dark bars on each segment (8.2%). The anterior and posterior surfaces of the thighs are pale brown, with a few darker flecks. The venter is either uniformly pale cream (66.6%), has dark flecks on the throat and chest (29.2%), or has a dark gray throat in one male (4.2%). A diffuse dark brown canthal stripe is present in 87.5% of the specimens; the margin of the upper lip is pale in 79.3%. Two individuals (8.3%) have a dark brown interorbital bar.

COLOR IN LIFE

The flanks and dorsum of the head and body are grayish tan. Most individuals have pale to dark green and black flecks or reticulations on the dorsal surfaces of head, body, and limbs (Fig. 12.44A). Some individuals have a few creamy white lichenous spots on the dorsal surfaces of the head and body (Fig. 12.44B). The dorsal surfaces of the first and second fingers are yellowish tan. The venter is creamy tan, with scattered brown flecks; the ventral surfaces of the limbs are yellowish tan. The canthal and supratympanic stripes are black, bordered with green. The tympanum is dark brown; the margin of the upper eyelid is green. Juveniles have a green dorsum, with or without golden flecks; black flecks are absent.

MEASUREMENTS

Males are smaller than females, but the smallest females (snout–vent lengths of 33.8 and 34.0 mm) are sexually mature and within the range of variation of males (Table 12.21). Although the average size of males is significantly smaller than that of females (ANOVA, $P = 0.001$), the proportions of their measurements are not significantly different.

CRANIAL OSTEOLOGY

No skeletal preparations are available.

Life History

The eggs of *Gastrotheca piperata* hatch as tadpoles, and these are released from the female's pouch at Stages 35 and 36. Most species of tadpole-producing *Gastrotheca* (e.g., *G. marsupiata*, *pseustes*, and *riobambae*) release tadpoles at Stages 30–32, but parturition of tadpoles by three species in Colombia (*G. argenteovirens*, *dunni*, and *trachyceps*) takes place when the tadpoles are in Stages 35–37. Thirteen females of these three species had snout–vent lengths of 42.9–69.8 mm ($\bar{x} = 57.0 \pm 10.3$), and were brooding 20–55 eggs ($\bar{x} = 38.2 \pm 4.5$) that were 4.2–6.0 mm ($\bar{x} = 5.1 \pm 0.3$) in diameter each. One female of *G. piperata* having a snout–vent length of 43.1 mm contained 51 eggs in the pouch. Thus the number and sizes of eggs and the stage of development at parturition in *G. piperata* is much the same as in these three Colombian species.

Gastrotheca piperata seems to reproduce at least throughout the rainy season; brooding females and juveniles were observed from November to March. In December 1994 at Sehuecas, Departamento de Cochabamba, Bolivia, during heavy rains females released

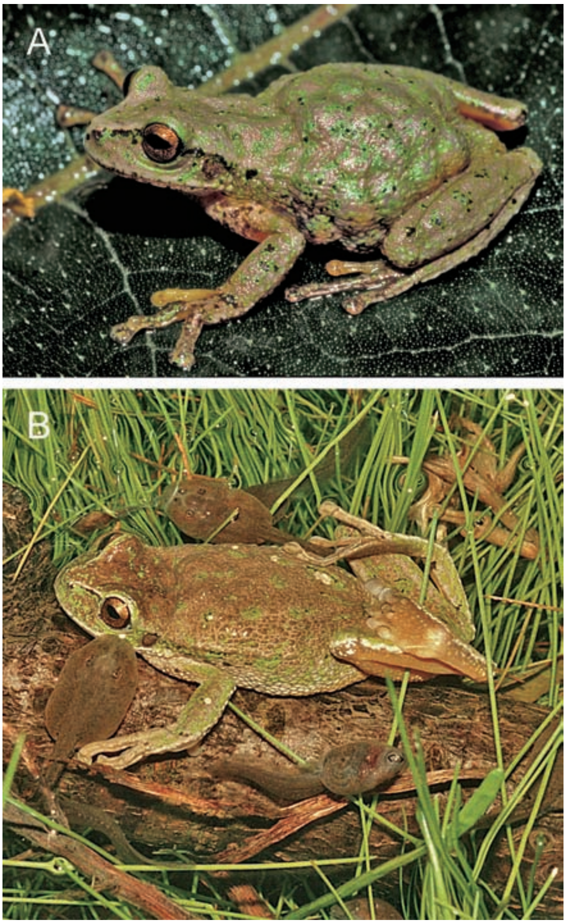

Fig. 12.44 *Gastrotheca piperata*. A: ZFMK 66838 (holotype), female, 34.0 mm SVL, Sehuecas, 2150 m, Cochabamba, Bolivia. B: female, La Siberia, Cochabamba, Bolivia (note the mature tadpoles). Photos by J. Köhler (A) and K. H. Jungfer (B), KUDA.

Table 12.21 Univariate statistics for adults of *Gastrotheca piperata*

	Males (n = 4)			Females (n = 17)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length**	34.1	31.1–36.3	2.33	39.7	33.8–46.8	3.55
Tibia length	15.8	14.9–16.4	0.63	19.5	17.4–22.0	1.43
Foot length	16.0	14.9–17.8	1.25	19.2	17.4–21.7	1.29
Head length	11.3	10.6–11.9	0.72	13.0	11.5–14.9	0.98
Head width	11.8	10.8–12.6	0.99	13.6	12.0–15.2	0.95
Interorbital distance	4.2	3.7–4.6	0.44	4.4	3.9–5.0	0.33
Eyelid width	3.4	3.2–3.8	0.26	3.8	3.1–4.5	0.39
Internarial distance	2.6	2.3–3.0	0.30	3.1	2.7–3.6	0.31
Eye diameter	4.1	3.8–4.4	0.25	4.4	3.9–5.1	0.37
Eye–nostril distance	3.8	3.7–3.9	0.08	3.9	3.2–4.5	0.37
Orbit–jaw distance	1.9	1.8–2.0	0.10	2.0	1.5–2.3	0.20
Nostril–jaw distance	2.6	2.4–3.1	0.32	2.8	2.3–3.5	0.32
Tympanum diameter	2.1	1.8–2.5	0.30	2.5	2.0–3.0	0.31
Thumb length	5.8	5.5–6.2	0.33	6.7	6.1–8.3	0.67
Third finger length	11.1	10.8–11.7	0.44	13.3	11.8–15.4	1.13
Disc width	1.7	1.3–1.9	0.26	2.1	1,4–2.6	0.49

**Differences between the means of the sexes are significant (ANOVA, $P = 0.001$).

tadpoles into small puddles and roadside ditches. The opening of the brood pouch was widened by the female inserting her feet into the pouch. In one case freshly released larvae accumulated around the female, and one tadpole moved back into the pouch; this suggests that olfactory substances are involved (Köhler et al., 1995). Females with approximately six to eight living larvae in their pouches were common; the release of tadpoles presumably does not necessarily occur all at once.

Tadpoles

A typical tadpole in developmental Stage 36 (KU 291625) has a body length of 7.2 mm, and a total length of 19.2 mm. In dorsal view the body is ovoid, and is blunt posteriorly. The body abruptly narrows anterior to the orbits to a nearly truncate snout; there are slight lateral indentations from just posterior to the orbits to midlength of the body. The greatest width of the body is at the level of the orbits and in the midgut region. The body is highest at about four-fifths its length; it gradually diminishes in height to the level of the orbits, and abruptly decreases in height from the level of the nares to the snout. The throat is slightly concave. The eyes are small, situated dorsolaterally, and slightly inclined anterolaterally. The interorbital distance is 1.1 mm. The distance from the snout to the anterior edges of the orbits is 1.3 mm. The nostrils are large, with an elevated rim; the nostrils are situated dorsolaterally, and are protuberant anterolaterally about midway between the tip of the snout and the orbits. The spiracle is sinistral, with its base is just left of the midventral line; it is curved posterolaterally, and is attached to the body wall throughout its length. The spiracular opening is directed dorsolaterally well below midheight of the body. The vent tube is dextral and elongately cone-shaped, with a transverse aperture; it is attached throughout its length to the ventral fin.

The caudal musculature is slender, and gradually tapers from its base to a pointed tip just proximal to the end of the fin. The dorsal fin originates on the base of the caudal musculature, and increases in height on the proximal one-fourth of the tail; it maintains equal height throughout the middle half of the tail, and gradually diminishes to a bluntly rounded tip. The ventral fin originates on the body wall, and is highest at about two-thirds the length of the tail. At midlength of the tail, the dorsal fin and caudal musculature are equal in height; the ventral fin is about two-thirds the height of the caudal musculature.

The oral disc is directed more ventrally than anteriorly; its width is about 40% of the greatest width of the body. The median one-fourth of the anterior labium is bare; elsewhere the labia bear a single row of long blunt marginal papillae, but there are two alternating rows posterolaterally; submarginal papillae are absent. There are two upper and three lower rows of labial teeth; the first lower row is interrupted medially. The tooth rows are long, and extend to the marginal papillae; the denticles are long and slender; the third lower tooth row is slightly shorter than the others, and has smaller denticles. The jaw sheaths are moderately massive, and are finely serrate. The anterior sheath is broadly arch-shaped, with long slender lateral processes; the posterior sheath is broadly V-shaped.

In preservative the body is dark brown both above and laterally. The anterior part of the belly is cream, with minute brown flecks; the posterior part is gray. The caudal musculature is brown; the fins are tan. In life the dorsal and lateral surfaces of the body are brown to olive tan; the caudal musculature is tan.

Advertisement Call

The call consists of a long pulsed note, repeated at regular intervals. Amplitude increases within the note, with maximum energy at its end. These long notes have a slight upward frequency modulation; they are sometimes followed by one to three short secondary notes, each containing only one pulse, which is equal in duration to a pulse within a long note. Numerical parameters are as follows (range followed by mean ± standard deviation in parentheses): calls per minute, 23–27 (24.98 ± 1.39); call duration, 657–965 milliseconds (744.81 ± 76.78); pulses per note (within long notes), 28–41 (33.00 ± 4.41); pulses per second (within long notes), 40.78–44.72 (42.08 ± 1.61); pulse duration, 9–15 milliseconds (10.77 ± 1.69); interval between long note and secondary note, 139–213 milliseconds (172.40 ± 26.52); dominant frequency range, 1400–2800 Hz; maximum call energy, 1883–2125 Hz (1995.9 ± 97.5).

Distribution and Ecology

Gastrotheca piperata is known from several localities along the eastern Andean slopes of Bolivia in Departamentos de Cochabamba and Santa Cruz, at elevations of 1850–2800 m (Fig. 12.45). The species inhabits humid upper montane forest and cloud forest, where annual precipitation is 3000–8000 mm (Kessler, 1999). Mean annual temperatures are between 12°C–15°C, but may drop to 0°C at night in June and July in areas above 2200 m.

The type locality is part of Carrasco National Park, which is characterized by steep slopes with inclinations of 40°–90° and the presence of many fast-flowing rivers, the largest being the Río Ivirizú. Natural landslides are common, resulting in a mosaic of forest formations at different successional stages. The vegetation consists of medium-height evergreen montane forest, with a high diversity of epiphytic bromeliads (e.g., *Tillandsia*, *Guzmania*), tree ferns (e.g., *Cyathea*, *Nephelea*), and bamboo (e.g., *Chusquea*). Human disturbance in the Sehuencas Valley is minor, restricted mainly to the banks of the Río Ivirizú (Köhler et al., 1995).

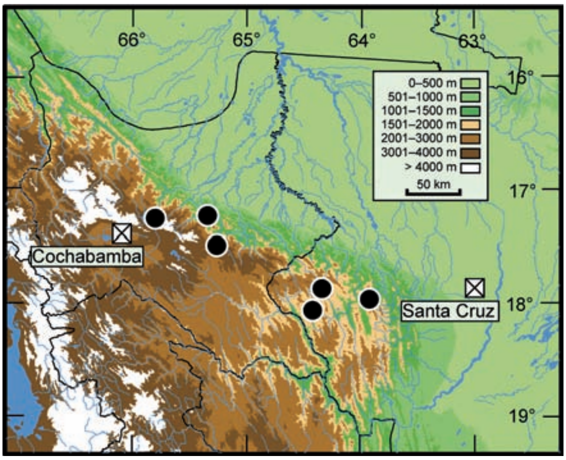

Fig. 12.45 Central Bolivia, showing the localities of known occurrences of *Gastrotheca piperata*.

Gastrotheca piperata is a nocturnal species, frequently encountered up to approximately 1.5 m above the ground on low vegetation during rain, but calling males were also heard from the canopy of smaller trees at dusk. One male was found at daytime in an epiphytic bromeliad. In captivity, a female *G. piperata* ingested a male strabomantid frog (*Pristimantis llojsintuta*) having a snout–vent length of about 20 mm.

Conservation Status

This species is categorized as being of Least Concern in the IUCN Red List.

Etymology

According to Duellman and Köhler (2005), the specific name *piperata* is a Latin adjective meaning "peppered"; it alludes to the small black flecks on the dorsum of the head, body, and limbs.

Remarks

Gastrotheca piperata has been confused with *G. marsupiata* (e.g., De la Riva et al., 1995, 2000). The latter species is mostly confined to non-forested high elevations above 3000 m, but it is similar in size and structure to *G. piperata*, which is known from forested slopes at elevations of 1850–2800 m.

A comparison of adults of *Gastrotheca marsupiata* from southern Peru and Bolivia with adults of *G. piperata* revealed no significant differences in sizes and proportions between the two species. Snout–vent length in 84 males of *G. marsupiata* is 30.6–41.6 mm ($\bar{x} =$

33.0 ± 2.20), and 30.9–49.6 mm ($\bar{x} = 37.7 \pm 4.08$) in 79 females, in contrast to 31.1–36.3 mm ($\bar{x} = 34.1 \pm 2.33$) in 4 males, and 33.8–46.8 mm ($\bar{x} = 39.7 \pm 3.55$) in 17 females of *G. piperata*. The mean tibia and foot lengths in relation to snout–vent length are slightly greater in *G. piperata* than in *G. marsupiata*; the mean width of the disc on the third finger in relation to the diameter of the tympanum is slightly less in *G. piperata* than in *G. marsupiata*.

The two species exhibit a few structural differences. The snout is more acutely rounded in dorsal view in *Gastrotheca marsupiata*, and the canthus rostralis is more acute in cross-section in *G. piperata*. The nostrils tend to be protuberant at the level of the anterior margin of the lower lip in *G. piperata*, and not protuberant at a level posterior to the margin of the lower lip in *G. marsupiata*. The tympanic annulus and supratympanic fold are tuberculate in *G. piperata* and are usually smooth in *G. marsupiata*. Low ulnar tubercles are present in *G. marsupiata* and are absent in *G. piperata*, which has moderately large subconical subarticular tubercles, in contrast to smaller round subarticular tubercles in *G. marsupiata*. The inner tarsal fold extends the full length of the tarsus in *G. piperata*, but it is weak and present only on the distal half of the tarsus in *G. marsupiata*. The smooth skin on the dorsum bears scattered small tubercles in *G. piperata*, whereas the skin varies from smooth to pustular but without tubercles in *G. marsupiata*, a species that also has slightly less webbing between the toes and a webbing formula of **I**2—2**II**2—3**III**(3–3^{-})—(3–4)**IV**(3–4)—(2–3)**V**.

The most distinctive differences between *Gastrotheca marsupiata* and *G. piperata* are in coloration, especially in life. The dorsal ground color of *G. piperata* is brown, grayish tan, silvery gray, green, bronze, or golden tan, with most individuals having dark green flecks or reticulations on the dorsum. This contrasts to the coloration of *G. marsupiata*, in which the dorsum is pale green or tan with darker green or brown spots, including an interorbital bar or T-shaped mark in 79% of 180 specimens from throughout the range; only 8.3% of the specimens of *G. piperata* have an interorbital bar. The flanks are marked with dark spots or mottling in 93% of the specimens of *G. marsupiata*, and by dark flecks in 75% of the ones of *G. piperata*.

Gastrotheca marsupiata and *G. piperata* exhibit significant differences in their life history. These are especially evident in the number of eggs brooded by females, sizes of eggs, and stage at hatching. Four brooding females of *G. piperata* having snout–vent lengths of 42.3, 37.9, 36.3, and 39.2 mm carried 29, 30, 31, and 33 eggs, respectively, with each egg 3.5–4.1 mm in diameter. In contrast, 12 brooding females of *G. marsupiata* in Región de Cusco, Peru, with snout–vent lengths of 33.7–43.3 mm ($\bar{x} = 39.2$) were carrying 63–167 eggs ($\bar{x} = 101.2$) having diameters of 2.9–4.0 mm ($\bar{x} = 3.3$) each. Eggs of *G. piperata* hatch at Stages 35 or 36; the hatchlings have body lengths of about 7.2 mm, and total lengths of about 19.2 mm. The smaller eggs of *G. marsupiata* hatch at Stage 30; the hatchlings have body lengths of 4.4 mm, and total lengths of 10.0 mm. One batch of tadpoles of *G. marsupiata* was raised in captivity; it required 28–34 days for them to reach Stage 36, but by that time they were much larger than tadpoles of *G. piperata* in Stage 36; body lengths of three tadpoles in Stage 36 were 16.7–16.8 mm, and total lengths were 42.0–42.9 mm.

There are minor differences in the structure of tadpoles of *Gastrotheca marsupiata* and *G. piperata*. The spiracular tube is shorter and directed posterodorsally in *G. marsupiata*, in which the vent tube is shorter and has a diagonal aperture, instead of the transverse opening in the longer conical tube in *G. piperata*. In the latter species, the oral disc has long marginal papillae; this contrasts with the shorter blunt papillae in *G. marsupiata*, in which each side of the anterior jaw sheath forms a sigmoid arch, compared with a broad uniform arch in *G. piperata*. In living tadpoles of *G. marsupiata* the dorsum of the body is olive green to grayish green, with or without faint metallic-green flecks; the causal musculature is greenish gray to tan; the fins are translucent, with or without yellowish-green flecks. Living tadpoles of *G. piperata* are olive tan dorsally and laterally; the caudal musculature is tan.

The calls of the two species have a similar structure, but they differ in temporal characteristics. Sinsch and Joermann (1989) recognized different kinds of calls in *Gastrotheca marsupiata*: a territorial call (termed advertisement call by these authors) of a single note, an aggressive call consisting of a long note followed by two to seven (usually three) short notes, and a breeding call consisting of a short note repeated every 1–10 seconds. The recordings of *G. piperata* (at 16.6°C) are equivalent to the aggressive call described by Sinsch and Joermann (1989) at 17°C, but with somewhat higher dominant frequencies (1400–2800 Hz, compared with 1400–1800 Hz in *G. marsupiata*) and a longer call duration (657–965 milliseconds, compared with 381–572 milliseconds in *G. marsupiata*). The number of pulses per long note (28–41 pulses in *G. piperata* and 16–42 pulses in *G. marsupiata*) and maximum call energy (1883–2125 Hz in *G. piperata* and 1550–2100 Hz in *G. marsupiata*) are much the same, but given the longer duration of the long notes in *G. marsupiata*, there are significant differences in pulse repetition rates: approximately 71.6 pulses per second in *G. marsupiata*, and 42.1 pulses per second in *G. piperata*.

Present knowledge of the distributions of *Gastrotheca marsupiata* and *G. piperata* suggests that the ranges of the two species are close to each other in some areas: in contact zones of the uppermost cloud forest, and in drier high-Andean vegetation. In Departamentos de Cochabamba and Santa Cruz, the ecotone between cloud forest with tree ferns and Andean vegetation with succulents may be only a few meters wide (e.g., at La Siberia). Thus it seems likely that *G. marsupiata* and *G. piperata* may occur sympatrically at the upper margin of cloud forest, where intermediate transitional conditions prevail.

Gastrotheca (*Gastrotheca*) *pseustes* Duellman and Hillis

Gastrotheca pseustes Duellman and Hillis, 1987:160.—Holotype: KU 203443 from 7.1 km [by road] N San Lucas, 2940 m (3°41′ S, 79°15′ W), Provincia de Loja, Ecuador.

Diagnosis

This medium-sized species attains a maximum snout–vent length of 62.4 mm. The tibia length is less than 50% of the snout–vent length, and is slightly shorter than the foot. The interorbital distance is slightly greater than the width of the upper eyelid. The skin on the dorsum is smooth to weakly pustular, not co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first and second fingers are equal in length, and bear discs that are slightly wider than the digits. The fingers are unwebbed; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is green, usually with a darker green or brown middorsal blotch. Markings on the head usually consist of a pale labial stripe and a dark canthal stripe. A pale dorsolateral stripe is absent. The flanks are tan or brown, with dark or pale spots. The venter is gray, usually with diffuse darker gray marks.

Gastrotheca pseustes is like *G. espeletia* and *G. riobambae* in having short limbs and small digital discs. It differs from *G. espeletia* in having the first and second fingers of equal length, and by having a broader and blunter snout. It differs from *G. riobambae* by having less webbing on the feet and a more truncate snout, and by lacking bold black spots or mottling on the ventral surface of the shank. Both *G. litonedis* and *G. plumbea* have color patterns like that exhibited by some specimens of *G. pseustes*, but both of the former species have larger digital discs and uniformly pale venters, as contrasted with the usually diffusely gray-spotted venter in *G. pseustes*, which differs from Peruvian species in being larger than any except *G. peruana*. *G. pseustes* differs from that species by having a round instead of an acuminate snout in dorsal view, more webbing on the feet, and in coloration. In *G. pseustes* the venter is gray, with or without diffuse dark spots; the posterior surfaces of the thighs are pale brown or blue, with or without dark spots. In *G. peruana* the venter is tan; the posterior surfaces of the thighs are brown, with or without pale spots.

Description

The following description is based on 157 specimens. The body is moderately robust; the maximum snout–vent length is 54.4 mm in males, and 62.4 mm in females. The head is slightly wider than long. The snout is rounded in dorsal view. and is inclined from the nostrils to its tip in lateral profile. The canthus rostralis is angular in cross-section. The loreal region is slightly concave; the lips are rounded. The top of the head is slightly concave. The interorbital distance is about 118% of the width of the upper eyelid. The internarial area is flat. The nostrils are slightly protuberant, and are directed laterally at the level of the anterior margin of the lower jaw and at the terminus of the canthus rostralis. The diameter of the eye is about equal to its distance from the nostril. The tympanum is vertically ovoid, and is separated from the eye by a distance equal to the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately heavy, and extends from the posterior corner of the eye to a point above the insertion of the arm.

The arm is moderately robust; ulnar tubercles are absent. The hand is moderate in size. The fingers are long, unwebbed, and bear small round discs; the width of the disc on the third finger is equal to the length of the tympanum. The relative lengths of the fingers are I = II < IV < III. The subarticular tubercles are moderately small and round; none are bifid. The supernumerary tubercles are few, small, round, and present only on the proximal segments of the fingers. The palmar tubercle is bifid; the prepollical tubercle is elongate and flattened; the thumb bears a brown nuptial excrescence in breeding males. The hind limb is moderately short and robust. The tibia length is 42.7%–47.8% ($\bar{x}$ = 44.7%) of the snout–vent length; the foot length is 45.3%–47.6% ($\bar{x}$ = 46.7%) of the snout–vent length. A calcar is absent; the inner tarsal fold is low, and is evident only on the distal one-third of the tarsus. The outer metatarsal tubercle is small and subconical; the inner metatarsal tubercle is ovoid, flat, and not visible from above. The toes are long. The relative lengths of the toes are I < II < III = V < IV. The toes are about one-third webbed; the webbing formula is **I**2^+—2^+**II**2—(2–2^+)**III**(2–2^+)—(3^-–3^+)**IV**(3^-–3^+)—2**V**. The subarticular tubercles are small and round; the supernumerary tubercles are small, round, and present only on the proximal segments.

The texture of the skin on the dorsal surfaces of the head, body, and limbs is variable: smooth (8%), areolate (33%), granular (34%), or pustular (25%). The skin on the flanks is areolate; the skin on the belly and ventral surfaces of the thighs is granular. Eyelid tubercles are absent. Cloacal folds and tubercles are absent. The opening of the brood pouch is U-shaped, with the anterior border at the level of the sacrum. The dentigerous processes of the vomers are transverse, and are narrowly separated medially between the small round choanae. Each process bears five to eight teeth.

COLOR IN PRESERVATIVE

The dorsal surfaces of the head, body, forelimbs, shanks, feet, and distal parts of the digits, as well as the loreal region, are bluish gray or dull tan. A labial stripe usually (92%) is present, but a supracloacal stripe is present in only 18% of the individuals. The dorsal surfaces of the proximal parts of the hands, upper arms, and thighs are creamy tan to pale gray. A cream canthal stripe usually (83%) is bordered below by a narrow brown line that extends from the tip of the snout through the nostril and along the outer edge of the eyelid, and is continuous with the dorsolateral line along the supratympanic fold; the dorsolateral line extends to the groin in some specimens. A pale cream dorsolateral stripe extends from the upper eyelid to the sacral region in 25% of the specimens. The dorsum of the body either lacks dark markings (20%) or has dark green or brown markings consisting of paravertebral longitudinal marks (55%), irregular spots (21%), or a middorsal mark (4%). The dorsal surfaces of the shanks are either uniformly bluish gray (28%) or are marked with dark green or brown spots (27%) or transverse bars (45%). The flanks are brown or gray, with darker spots (37%) or pale spots posteriorly (26%). The anterior and posterior surfaces of the thighs are either uniformly blue or bluish brown (68%) or have dark spots (32%). The chest and belly are uniformly dull gray (40%) or have diffuse darker gray markings (60%). The ventral surfaces of the limbs are uniformly gray; the vocal sac is pale gray, with dark flecks.

COLOR IN LIFE

Although most individuals of *Gastrotheca pseustes* have a green dorsum with darker green or brown markings, the colors are highly variable (Fig. 12.46). This is exemplified by the following descriptions of living individuals from Ecuador.

KU 120676–705 from Cuenca, Provincia de Azuay.—The dorsum is green, gray, or brown, with chocolate-brown markings edged with bronze. The centers of the markings commonly are bright green, especially on the limbs. The flanks are gray or bronze, with a bluish-green suffusion; the posterior surfaces of the thighs are bluish green; the venter is white to dull bronze cream (J. D. Lynch field notes, 19 June 1968).

KU 120741–56 from 10 km SW Mocha, Provincia de Tungurahua.—The dorsum is either forest green with black spots edged with brown, brown with green spots, or uniformly brown. The flanks and posterior surfaces of the thighs are bluish green (J. D. Lynch field notes, 24 June 1968).

KU 138624–27 from 3 km S Azogues, Provincia de Cañar.—The dorsum is uniformly yellowish green, with a dark brown suffusion on the head. One individual is tan, with copper-colored blotches. The flanks and posterior surfaces of the thighs are grayish blue (greenish blue in the tan specimen). The venter is creamy white, with gray blotches; the labial stripe is white (T. H. Fritts field notes, 8 June 1970).

KU 142609–13 from Saraguro, Provincia de Loja.—The dorsum is tan or green, with dark green or dark brown blotches. The green blotches on green individuals changed to brown. One uniformly green frog changed to uniformly tan. The canthal and dorsolateral stripes are creamy bronze. The axilla, groin, and hidden surfaces of the thighs are conspicuously marked with bright blue. The belly is creamy gray, with gray spots; the throat is gray (W. E. Duellman field notes, 24 July 1971).

KU 142616–19 from 2.5 km S Guaranda, Provincia de Bolívar.—The dorsum is green, with dark green blotches outlined with dark brown and cream. The labial and dorsolateral stripes are creamy bronze. The axilla, groin, and posterior surfaces of the thighs are blue, with cream and black flecks on the latter. The venter is creamy gray, with black flecks (W. E. Duellman field notes, 12 July 1971).

KU 164238 from 2.5 km S Palmira, Provincia de Chimborazo.—The dorsum is green, with bronze-

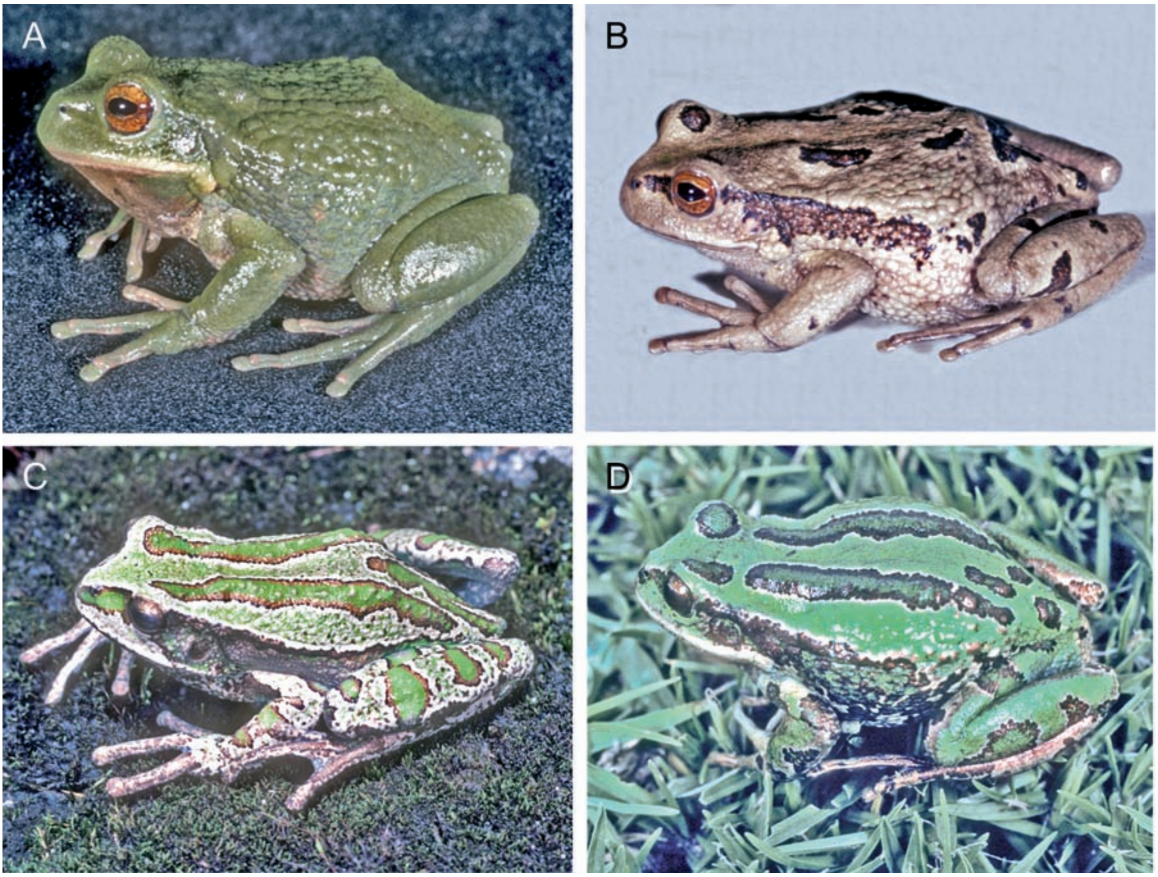

Fig. 12.46 *Gastrotheca pseustes*. A: KU 143095, male, 47.8 mm SVL, Papallacta, Napo, Ecuador. B: KU 146750, female, 45.8 mm SVL, Mulaló, Cotopaxi, Ecuador. C: KU 203458, female, 73.8 mm SVL, 3.7 km S Saraguro, 2800 m, Loja, Ecuador. D: KU 203538, male, 52.2 mm SVL, 4 km N Zhud, 3040 m, Cañar, Ecuador. Photos by W. E. Duellman.

tan longitudinal marks, labial stripe, and dorsolateral stripe. The groin and posterior surfaces of the thighs are dull blue; the venter is creamy gray; the vocal sac is gray (W. E. Duellman field notes, 11 March 1975).

KU 202691–92 from 10 km NW Girón, Provincia de Azuay.—The dorsum is pale greenish tan and the flanks are tan, or the dorsum is green with dark brown dorsal and lateral markings. The dorsolateral stripe is bronze; the axilla and groin are bluish gray (W. E. Duellman field notes, 7 March 1984).

KU 203459 from 11.5 km SE Gualaceo, Provincia de Azuay.—The dorsum is tan, with chocolate-brown markings and a greenish suffusion posteriorly. The labial stripe is cream. The groin and hidden surfaces of the thighs are dull bluish gray; the venter is creamy gray, with diffuse gray spots (W. E. Duellman field notes, 4 March 1984).

KU 203461–64 from Laguna de Zurucuchu, Provincia de Azuay.—The dorsum is emerald green, with each of four individuals marked as follows: (1) uniformly green, (2) olive-green markings narrowly outlined with bronze tan, (3) brown markings narrowly outlined by bronze tan, and (4) bronze dorsolateral stripe and paravertebral marks (W. E. Duellman field notes, 5 March 1984).

One female (KU 204032), having a dull green dorsum with dark brown markings outlined with bronze tan, produced tadpoles that were raised in the laboratory; 62 of these metamorphosed into young having a tan dorsum with brown markings.

Nearly all specimens of *Gastrotheca pseustes* have at least a suffusion of blue in the axilla and groin and on the hidden surfaces of the thighs; in some individuals this blue is intense. The venter is uniformly dull cream or creamy gray in some individuals, but in most individuals diffuse gray flecks or spots are evident. These

Table 12.22 Univariate statistics for adults of *Gastrotheca pseustes*

	Males (n = 87)			Females (n = 69)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length**	46.4	38.3–54.4	3.68	49.6	36.0–62.4	5.69
Tibia length**	20.4	16.6–23.9	1.69	22.5	15.6–32.5	3.40
Foot length	21.7	17.9–25.8	1.89	23.2	16.2–28.5	2.63
Head length**	14.7	12.3–17.5	1.18	15.5	11.6–19.4	1.71
Head width**	16.3	13.6–19.9	1.30	17.4	13.3–22.7	2.07
Interorbital distance**	4.2	3.2–6.9	0.50	4.8	3.1–8.3	1.16
Eyelid width	3.8	2.9–4.8	0.40	3.8	2.8–4.7	0.41
Internarial distance**	2.9	2.5–3.7	0.25	3.1	2.4–3.9	0.34
Eye diameter**	4.3	2.7–5.3	0.36	5.6	3.1–5.9	0.62
Eye–nostril distance**	3.5	2.9–4.6	0.32	3.9	2.8–5.9	0.64
Orbit–jaw distance**	2.0	1.5–2.6	0.22	2.2	1.6–2.9	0.34
Nostril–jaw distance**	3.0	2.5–3.7	0.27	3.2	2.3–4.2	0.41
Thumb length**	8.5	6.5–9.9	0.77	9.2	6.5–11.6	1.13
Third finger length	15.0	12.2–18.6	1.26	15.9	9.2–19.6	1.94
Disc width**	2.0	1.2–2.9	0.34	2.2	1.4–3.1	0.36

**Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

are not well-defined spots or mottling, as in *G. riobambae*, and the ventral surfaces of the limbs are never mottled, as in that species. Descriptions of the iris color in life vary from deep gold to bronze or copper, with black flecks or reticulations.

MEASUREMENTS

The means of most measurements of females are significantly larger than those of males (Table 12.22). The largest male included in the analysis has a snout–vent length of 54.4 mm. One gigantic male (KU 203458) from Saraguro has a snout–vent length of 74.8 mm, 12.4 mm larger than the largest female. The identity of this specimen was confirmed allozymically, but it was not included in any of the morphometric analyses.

CRANIAL OSTEOLOGY

The sphenethmoid is smooth and superficially unsculptured, in contrast to the remainder of the skull table, which bears a semicoarse pit-and-ridge pattern of dermal sculpturing. The nasals articulate medially, and are synostosed to one another as well as to the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals have a complete articulation medially; the supraorbital flange is narrow; the otic flange is large. A temporal arcade is absent. The frontoparietal extends over the anterior epiotic eminence; the carotid canal is partially closed, and posteriorly exits the skull roof through the frontoparietal. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for more than three-fourths the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is long. The postorbital process of the maxilla is massive, and has a broad horizontal articulation with the wide zygomatic process of the squamosal. The head of the squamosal has a narrow crest; the narrow otic plate articulates marginally with the crista parotica. The dorsal part of the stapedial footplate is two to three times the size of the ventral portion, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has a blunt terminus posterior to the level of the neopalatines. The sphenethmoid is ossified posterior to the midlength of the orbit, but is not synostosed with the prootic. The neopalatines are widely separated medially, and have an irregular ridge ventrally. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a long acuminate recurved process on the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located between the middle quadrants of the choanae.

Life History

Gastrotheca pseustes broods relatively small eggs, which hatch into tadpoles that complete their development in shallow ponds. Fourteen brooding females, having snout–vent lengths of 47.4–60.2 mm ($\bar{x} = 54.2$), were brooding 49–197 eggs ($\bar{x} = 109.1$), of which the ovarian diameter was 2.6–6.3 mm ($\bar{x} = 4.5$). Brooding females have been collected in January, February, March, June, and July. These months fall within the rainy season (November–August) in the Andes of central and southern Ecuador.

Tadpoles

A typical tadpole in Stage 35 (KU 203554) has a body length of 25 mm, and a total length of 67 mm. In dorsal view the body is ovoid, widest at about two-thirds the length of the body; the snout is bluntly rounded. In lateral profile the body is deepest posteriorly, where the height is about three-fourths the width of the body; the throat is convex; the snout is inclined from the nostrils to the bluntly rounded tip. The eyes are large, and are directed dorsolaterally. The interorbital distance is slightly less than half the width of the body at the level of the orbits. The nostrils are slightly closer to the eyes than to the tip of the snout. The spiracular tube is short and sinistral; its opening is directed posterodorsally on the ventrolateral surface at midlength of the body. The cloacal tube is short, broad, and median, with a transverse opening. The caudal musculature is robust, higher than the dorsal fin at midlength of the tail, and terminates gradually into a pointed tip well within the margin of the caudal fin. The dorsal fin arises gradually from the posterior edge of the body; the dorsal fin is slightly shallower than the ventral fin at midlength of the tail. The fins terminate in a bluntly rounded tip.

The width of the oral disc is about 40% of the width of the body. The disc is bordered laterally and ventrally by a single row of short blunt marginal papillae. There are two upper and three lower rows of labial teeth; the upper rows and first lower row are about equal in length; the second and third lower rows are progressively shorter; the second upper and first lower rows are narrowly interrupted medially. The upper jaw sheath is massive, and forms a broad arch; the lower sheath is V-shaped, with convexly curved arms. The lower sheath and median part of the upper sheath bear short blunt serrations.

The dorsum of the body is dark brown; the venter is bluish gray. The caudal musculature is tan proximally and dark brown distally; the fins have diffuse brown flecks.

Advertisement Call

The call consists of a low pitched note, usually followed by two or more short chuckles.

Distribution and Ecology

This species is widely distributed in the Cordillera Oriental and Cordillera Occidental of Ecuador, from the Equator south to high elevations north of the Loja Valley in southern Ecuador (Fig. 12.47). Its elevational range is 2200–4080 m. In the northern part of the range it seems to be confined to elevations above 3000 m, whereas in the south it ranges from 2200 to 3800 m.

The species is most abundant in páramo and subpáramo, where it inhabits moderately dry regions characterized by bunchgrasses and cushion plants. By day individuals have been found under stones in pastures and in páramo, in crevices between leaves of *Agave* plants, and in crevices in stone walls. *Gastrotheca pseustes* seems to be most common (or at least most easily found) in narrow irrigation ditches, where the frogs are on the banks of ditches overhung with vegetation. On cloudy or misty days males commonly call from ditches or from beneath stones. At night males have been found calling from open ground, branches of low bushes (e.g., *Baccharis*), margins of shallow ponds, and reeds in a lake. Tadpoles have been found in shallow grassy ponds.

Conservation Status

In the IUCN Red List, *Gastrotheca pseustes* is designated as Threatened; even though it occurs in several protected areas in Ecuador, populations are declining. Chytridiomycosis has been confirmed in this species, and probably is the main cause of its decline (Coloma et al., 2004).

Etymology

The specific name *pseustes* is Greek, meaning "liar"; the name was used in reference to the phenotypic similarity of the species to *Gastrotheca riobambae*, with which it had been confused previously (Duellman and Hillis, 1987).

Remarks

Gastrotheca pseustes is highly variable in size, structure, and coloration. Accordingly, the variation in the species was analyzed by comparing morphometric and descriptive characters in samples from 11 areas in the Andes of Ecuador. In an approximately north–south order, these areas are: Papallacta (including Paso de Guamaní), Occidental (cordillera west of Quito), Mulaló, Cotopaxi (localities west of Latacunga), Cotaló,

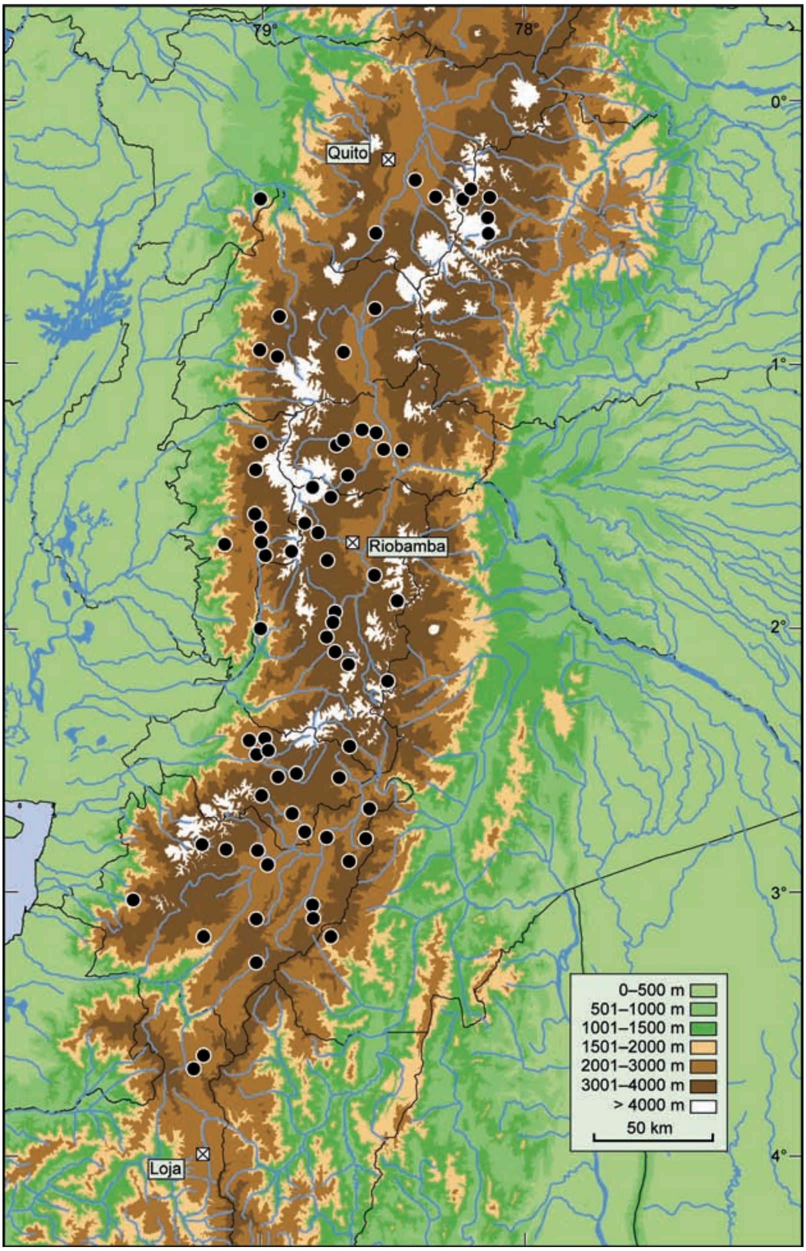

Fig. 12.47 Andean region of Ecuador, showing the localities of known occurrences of *Gastrotheca pseustes.*

Mocha, Guaranda, Guamote, Biblián, Cuenca, and Saraguro (Table 12.23).

MORPHOMETRICS

An analysis of variance and nonparametric tests revealed that sexual dimorphism was evident in various measurements in different populations (e.g., tibia length in Saraguro, head length and head width in Guaranda, head length and thumb length in Mulaló). The apparent absence of sexual dimorphism in most characters seems to be an artifact of the small sample size, since when all samples are pooled, significant differences between the means of the sexes were evident in all measurements except eyelid width (Table 12.22).

A principle components analysis of the measurements of frogs from all 11 populations revealed considerable overlap among the populations. Size was the principal contributing component in both sexes, which were analyzed separately. The principle component on the second axis was disc size versus all other characters in males, and interorbital distance and tym-

Table 12.23 Numbers of specimens of *Gastrotheca pseustes* from different localities used in the analyses. The morphometric analyses were based only on adults; the analyses of descriptive characters and color patterns were based on all specimens.

Population	Males	Females	Subadults	Total
Papallacta	10	15	2	27
Occidental	1	1	1	3
Mulaló	3	9	4	16
Cotopaxi	6	1	0	7
Cotaló	3	2	0	5
Mocha	10	7	0	17
Guaranda	6	11	0	17
Guamote	3	2	0	5
Biblián	3	1	0	4
Cuenca	21	15	1	37
Saraguro	21	5	10	36
Totals	87	69	18	174

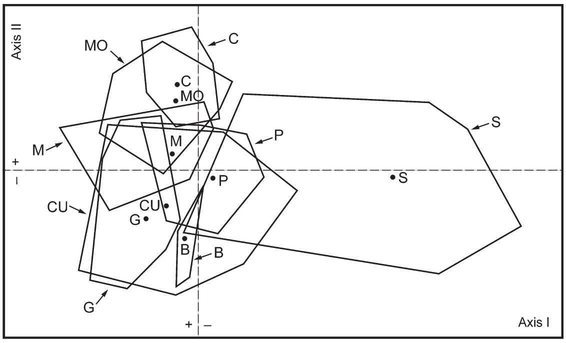

Fig. 12.48 Multivariate plot of a stepwise discriminant analysis of morphometrics of adult *Gastrotheca pseustes* from eight localities in the Ecuadorian Andes. The polygons encompass the dispersion of individuals, and the dots are the means of samples identified by the letters B = from Biblián (*n* = 4), C = from Cotopaxi (*n* = 7), CU = from Cuenca (*n* = 37), G = from Guaranda (*n* = 17), M = from Mulaló (*n* = 16), MO = from Mocha (*n* = 17), P = from Papallacta (*n* = 17), and S = from Saraguro (*n* = 27).

panum diameter versus head width and finger length in females. The third axis incorporated tympanum diameter versus snout–vent length in males, and disc size in females. These three axes accounted for 83% of the variation in males, and 87% in females.

A stepwise discriminant functions analysis showed that there is considerable overlap in various populations, but the sample from Saraguro has only minimal overlap with three other populations: Biblián, Cuenca, and Papallacta (Fig. 12.48). The jackknifed classification of this eight-step model correctly classified only 51.1% of the specimens according to population. In comparison with frogs in other populations, those from Saraguro are characterized by greater snout–vent and foot lengths, broader head width, larger interorbital distance, and a proportionately shorter third finger. Although there is great overlap among the rest of the samples, frogs from Cotopaxi and Mulaló have broader heads, greater interorbital distances, and shorter tibias than those from Cuenca and Guaranda. Frogs from the other samples are intermediate in these characters.

STRUCTURAL CHARACTERS

The dorsal skin texture of 142 of the specimens was characterized as smooth in 11 specimens from Cotopaxi, Cuenca, Mocha, and Occidental. The skin is areolate in 52 specimens, including all of those from Saraguro and 25 other specimens from Cotopaxi, Cuenca, Guamote, Guaranda, Mocha, Mulaló, and Papallacta. Granular dorsal skin occurs in 54 frogs from all populations except Cotaló, Occidental, and Saraguro. The webbing on the foot extends to a point between the antepenultimate and penultimate tubercles on the fourth toe in 127 specimens from all populations, including all specimens from Cotaló, Guamote, Mocha, Occidental, and Papallacta. The webbing extends to the penultimate tubercle in 27 specimens from Biblian, Cotopaxi, Cuenca, Guaranda, Mulaló, and Saraguro, and to the distal tubercle in 1 specimen from Saraguro. The webbing extends to the distal tubercle on the fifth toe except for 1 specimen from Saraguro, in which it reaches a point between the penultimate and distal tubercles.

COLORATION

A pale labial stripe is present in all but 12 specimens from Cuenca, Guaranda, Mocha, and Papallacta; the stripe extends ventrolaterally onto the flanks in 12 specimens from Guaranda, Mocha, Papallacta, and Saraguro. A dark canthal stripe is present in 128 specimens; it is absent in 27 specimens from all populations except Biblián, Cotaló, and Cuenca. The dorsum is tan to brown or various shades of green, usually with dark brown or dark green markings. Dorsal markings are absent in 30 specimens from all populations except Biblián and Guaranda. The most common dorsal pattern consists of paravertebral markings; these are present in 86 specimens from all populations, including all specimens from Mocha and Occidental. The pattern consists of dark mottling in 32 specimens from all populations except Papallacta, and dark flecks in 4 specimens from Cuenca, Mocha, and Mulaló. A narrow dark middorsal stripe is present in 1 specimen from Cuenca, and a broad middorsal stripe is present in 1 specimen from Guaranda and 3 from Saraguro. A dark interorbital bar is present in 1 specimen from Cotopaxi and 1 from Saraguro. A pale dorsolateral stripe is present in 38 specimens: Cuenca 1 (3% of sample from that locale), Guaranda 13 (76%), Mulaló 7 (44%), and Saraguro 17 (63%). The flanks are uniformly dark brown or gray in 29 specimens from all populations (including all specimens from Cotaló) except Saraguro. The flanks are pale gray or cream with dark spots in 56 specimens from all populations except Saraguro (27 specimens), in which the flanks are dark brown with cream spots, as they are in 11 specimens from Cuenca, 1 from Guaranda, and 1 from Mulaló. The anterior surface of the thigh is uniformly brown or gray in 43 specimens from all populations (including all specimens from Biblián and Cotaló) except Saraguro. The other 112 specimens have mottling or spots on the anterior surface of the thigh; this includes all specimens from Saraguro. The posterior surface of the thigh is uniformly brownish gray or bluish gray in 107 specimens and is marked with spots in 48 specimens, including all of those from Cotopaxi, Guamote, and Occidental. A pale supracloacal stripe is present in 27 specimens from Cuenca, Guaranda, Mocha, Mulaló, and Saraguro. The throat is dull gray to black in breeding males. Otherwise the venter is dusty cream to dull gray. A diffuse pattern is present in 93 specimens from all populations; this is in the form of spots in 52 specimens, flecks in 10 specimens, and a mixture of spots and flecks in 31 specimens.

The variation in morphometrics, structural characters, and coloration presents a geographic mosaic, except that the southernmost population, Saraguro, is somewhat more distinctive than the others in having (1) larger sizes, (2) broader heads, and (3) some consistent characteristics of color pattern, including dark flanks with pale spots and uniformly dark posterior surfaces of the thighs. Samples from most of the populations discussed above were subjected to allozymic analysis, which showed them to be conspecific (Duellman and Hillis, 1987). Ongoing analyses of molecular data suggest that there may be two species in what is now being called *Gastrotheca pseustes*.

Gastrotheca (Gastrotheca) psychrophila Duellman

Gastrotheca psychrophila Duellman, 1974a:15.—Holotype: KU 120760 from ridge between Loja and Zamora, 2850 m, 13–14 km [by road] E Loja, Provincia de Loja, Ecuador.
Gastrotheca (*Duellmania*) *psychrophila*—Dubois, 1987:33.

Diagnosis

In this medium-sized species, adults attain a snout–vent length of 63.5 mm. The tibia length is less than 55% of the snout–vent length, and is slightly longer than the foot. The interorbital distance is noticeably wider than the upper eyelid. The skin on the dorsum is smooth or areolate, not co-ossified with the skull (co-ossified with the frontoparietals in large females), and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is shorter than the second; the discs on the fingers are noticeably wider than the digits. The fingers are webbed basally; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the fifth toe. The dorsum is uniformly brown, black, or dull green. Markings on the head usually consist of only a pale labial stripe. A pale dorsolateral stripe is absent. The flanks are uniformly dark gray or brown; the venter is creamy gray.

Gastrotheca psychrophila superficially resembles *G. ruizi*, which differs by having an acuminate snout, pale green paravertebral marks, and the first and second fingers equal in length. The tadpoles of *G. psychrophila* differ from those of the other species (except *G. espeletia*) by having the dorsal fin arise abruptly from the body; the tadpoles of *G. espeletia* have only a single row of labial papillae ventromedially, whereas there are two alternating rows in *G. psychrophila*.

Description

The following description is based on 15 specimens. The body is moderately robust. The maximum snout–vent length is 50.0 mm in males, and 63.5 mm in females. The head is slightly wider than long, and nearly as wide as the body. The snout is broadly rounded in dorsal view, and is bluntly rounded in profile. The canthus rostralis is rounded in cross-section. The loreal region is barely concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 170% of the width of the upper eyelid. The internarial area is flat. The nostrils are not protuberant, and are directed dorsolaterally at a level posterior to the anterior margin of the lower jaw. The diameter of the eye is about equal to its distance from the nostril. The tympanum is round, and is separated from the eye by a distance equal to the diameter of the tympanum. The tympanic annulus is distinct and smooth; the supratympanic fold is moderately weak, and extends from the posterior corner of the orbit to a point above the insertion of the arm.

The arm is moderately robust, and lacks ulnar tubercles. The hand is moderate in size. The fingers are long, and bear moderately large round discs; the width of the disc on the third finger is slightly greater than the diameter of the tympanum. The first finger is shorter than the second. The relative lengths of the fingers are I < II < IV < III. Webbing is present basally between Fingers II, III, and IV. The subarticular tubercles are large and round; the distal tubercle on the fourth finger is weakly bifid in some specimens. The supernumerary tubercles are moderately large, round, and present only on the proximal segments. The palmar tubercle is trifid; the prepollical tubercle is elongate; in breeding males the thumb bears nuptial excrescences. The hind limb is moderately robust. The tibia length is about 50% of the snout–vent length; the foot length is about 48% of the snout–vent length. A calcar and outer tarsal tubercles and folds are absent. The inner tarsal fold is curved on the distal two-thirds of the tarsus. The outer metatarsal tubercle is small and subconical; the inner metatarsal tubercle is small, flat, elliptical, and not visible from above. The toes are long. The relative lengths of the toes are I < II < III < V < IV. The toes are about two-fifths webbed; the webbing formula is **I**2—2**II**2—3**III**2—(3–3^+) **IV**(3–3^+)—2**V**. The subarticular tubercles are moderately large and round; the supernumerary tubercles are small, round, and present only on the proximal segments.

The skin on the dorsal surfaces of the head, body, and limbs is smooth (29%) or areolate (71%); in large females, the skin is co-ossified with the frontoparietals; the skin on the flanks is areolate; the skin on the belly and proximal posteroventral surfaces of the thighs is granular. A pair of tubercles is present below the cloacal opening. The opening of the brood pouch is U-shaped, with the anterior edge at the posterior edge of the sacrum. The dentigerous processes of the vomers are inclined posteromedially, and are narrowly separated medially between the small round choanae. Each process bears four to seven teeth.

COLOR IN PRESERVATIVE

The dorsal surfaces of the head, body, and limbs usually (86%) are dark gray or greenish brown; dark spots are present in 7% of the specimens; a dark middorsal mark is evident in another 7% of the specimens. A pale labial stripe usually (71%) is present. A dark canthal stripe and pale dorsolateral and supracloacal stripes are absent. The flanks usually (86%) are dark gray or brown, or have pale spots (14%). The anterior and posterior surfaces of the thighs are uniformly dark bluish gray. The ventral surfaces are uniformly pale creamy gray; the vocal sac is dark gray.

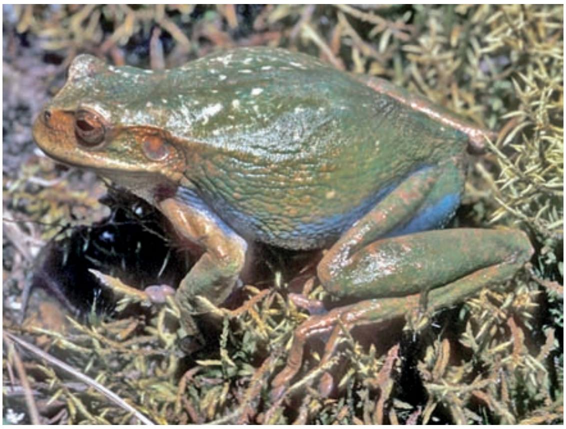

Fig. 12.49 *Gastrotheca psychrophila* (KU 164233), female, 63.5 mm SVL, Abra de Zamora, 13 km E Loja, 2850 m, Loja, Ecuador. Photo by W. E. Duellman.

COLOR IN LIFE

These frogs usually are rather dull colored, with a coppery-bronze iris reticulated with black (Fig. 12.49). There is considerable metachrosis, as evidenced from the following descriptions of living individuals from the vicinity of the type locality.

KU 120760–61.—The dorsum is dull green to bronze; the flanks are bronze above and blue below. The hidden surfaces of the limbs are blue. The venter is rose gray (J. D. Lynch field notes, 10 June 1968).

KU 142631–33.—Three adults were brownish black above and below when collected by day; the flanks and posterior surfaces of the thighs were dark bluish black. Later they changed to copper on the dorsal surfaces; the venter was grayish brown. The palmar and plantar surfaces and the pectoral and gular regions were dark brown black. The labial stripe was bronze. Bluish-purple coloration was evident in the axilla and groin, and on the anterior and posterior surfaces of the thighs (W. E. Duellman field notes, 21 July 1971).

KU 164233–34.—A female had a bright green dorsum, with cream flecks. The hands and feet were tan; the flanks and hidden surfaces of the limbs were bright blue. A male was dark brown; later it changed to pale brown. The flanks and hidden surfaces of the limbs were dark blue, with bright orange spots in the groin and on the hidden surfaces of the thighs (W. E. Duellman field notes, 8 March 1975).

Table 12.24 Univariate statistics for adults of *Gastrotheca psychrophila*

	Males ($n = 3$)			Females ($n = 9$)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length	47.7	45.8–49.9	2.06	52.5	43.9–63.5	6.61
Tibia length	24.0	23.4–24.6	0.60	26.2	23.5–30.7	3.21
Foot length	22.7	21.3–24.0	1.36	25.2	20.0–31.8	4.54
Head length	16.5	16.3–16.7	0.21	17.5	15.8–20.5	1.93
Head width	18.6	18.1–19.0	0.47	19.7	18.1–22.8	2.02
Interorbital distance	5.8	5.5–6.0	0.27	6.3	5.7–7.3	0.65
Eyelid width	3.3	2.7–3.6	0.52	3.7	2.6–4.2	0.50
Internarial distance	2.5	2.3–2.7	0.20	2.8	2.4–3.5	0.39
Eye diameter	4.4	3.9–4.6	0.23	4.4	3.7–4.8	0.34
Eye–nostril distance	4.5	4.3–4.8	0.25	4.6	4.1–5.4	0.42
Orbit–jaw distance	2.6	2.4–2.9	0.27	2.7	2.3–3.2	0.35
Nostril–jaw distance	3.5	3.1–3.9	0.40	3.8	3.2–4.8	0.54
Tympanum diameter	2.6	2.4–2.7	0.15	2.7	2.2–3.2	0.30
Thumb length	8.6	8.2–8.8	0.35	9.4	7.2–11.5	1.63
Third finger length	16.5	15.9–16.9	0.53	16.9	14.7–21.0	2.57
Disc width	2.7	2.5–2.9	0.21	2.8	2.3–3.5	0.45

MEASUREMENTS

Females are larger than males (Table 12.24). The fact that an ANOVA revealed no significant differences between the means of measurements of males and females probably is attributable to the small sample size of males.

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous semicoarse pattern of shallow pits and low rounded ridges. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals are completely articulated medially, and have a wide supraorbital flange and a moderate-sized otic flange. A temporal arcade is absent. The frontoparietal covers the anterior epiotic eminence and part of the posterior eminence, to which it is partially fused; thus the carotid canal is partially open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for about half the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is long. The postorbital process of the maxilla is massive, and has a broad horizontal articulation with the wide zygomatic process of the squamosal. The head of the squamosal has a narrow crest; the narrow otic plate articulates marginally with the crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in size, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are narrowly separated medially, and are smooth ventrally. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a long blunt process on the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located between the posterior margins of the choanae.

Life History

This species produces tadpoles, but no brooding females are known. Females collected in March and June have small ovarian eggs. Males have been heard calling by day in March, May, June, and July. Tadpoles have been found in shallow pools in March and May; metamorphosing young have been found in the same months. Some tadpoles reach an extremely large size. Four tadpoles in Stages 43 and 44 have body lengths of 33.6–34.6 mm ($\bar{x} = 34.0$), and total lengths of 81.8–83.9 mm ($\bar{x} = 82.8$). Eight recently metamorphosed young have snout–vent lengths of 23.7–26.9 mm ($\bar{x} = 25.2$).

Tadpoles

A typical tadpole in Stage 25 (KU 203601) has a body length of 24.5 mm, and a total length of 64.0 mm. In dorsal view the body is elongately ovoid, widest at about 80% of the length of the body, and has a slightly rounded snout. In profile the body is highest at two-thirds its length, and is higher than wide. The snout is inclined from the nostrils to a rounded tip. The throat is convex. The eyes are small, and are directed dorsolaterally. The interorbital distance is slightly less than one-half the width of the body at the level of the orbits. The nostrils are slightly closer to the eyes than to the tip of the snout, and are directed anterolaterally. The spiracular tube is small, with the opening directed posterodorsally on the ventrolateral surface at about midlength of the body. The cloacal tube is median, and is a short broad cone, with a transverse opening. The caudal musculature is moderately robust; its height is less than that of the dorsal fin at midlength of the tail. The caudal musculature terminates in an acute tip well within the margin of the caudal fin. The dorsal fin arises abruptly from the posterior edge of the body. The dorsal and ventral fins are equal in depth at midlength of the tail, and terminate abruptly in a bluntly rounded tip.

The width of the oral disc is about 33% of the width of the body. The disc is bordered laterally and ventrally by two alternating rows of short blunt marginal papillae. There are two upper and three lower rows of labial teeth; the rows are about equal in length; the first lower row is narrowly interrupted medially. The upper jaw sheath forms a continuous arch; the lower sheath is massive, and is broadly V-shaped. The sheaths bear minute pointed serrations.

The dorsum of the body is olive tan, with fine grayish-black flecks. The venter is gray, with white flecks; the caudal musculature is pale tan. The iris is bronze.

Advertisement Call

The call is unknown.

Distribution and Ecology

This species is known from a limited area, at an elevation of 2750–2850 m on a ridge (the Abra de Zamora) between Loja and Zamora in the Cordillera Oriental in southern Ecuador, but it also has been reported from Loja at 2150 m (Fig. 12.50). Most individuals have been found by day in large terrestrial bromeliads on the east slope of the ridge. Two adults and some juveniles were under stones by day, and one individual was on a bromeliad leaf at night. Tadpoles have been found in small shallow grassy ponds at the crest and on the western slope of the ridge.

Conservation Status

In the IUCN Red List, *Gastrotheca psychrophila* is listed as Threatened, because of conversion of its habitat to pine tree plantations, and an expansion of agriculture involving both crops and livestock. The habitat at the type locality of this species was greatly disturbed by the construction of a highway across the ridge in 1984.

Etymology

The specific name is derived from the Greek *psychros*, meaning "cold," and the Greek *philos*, meaning "having

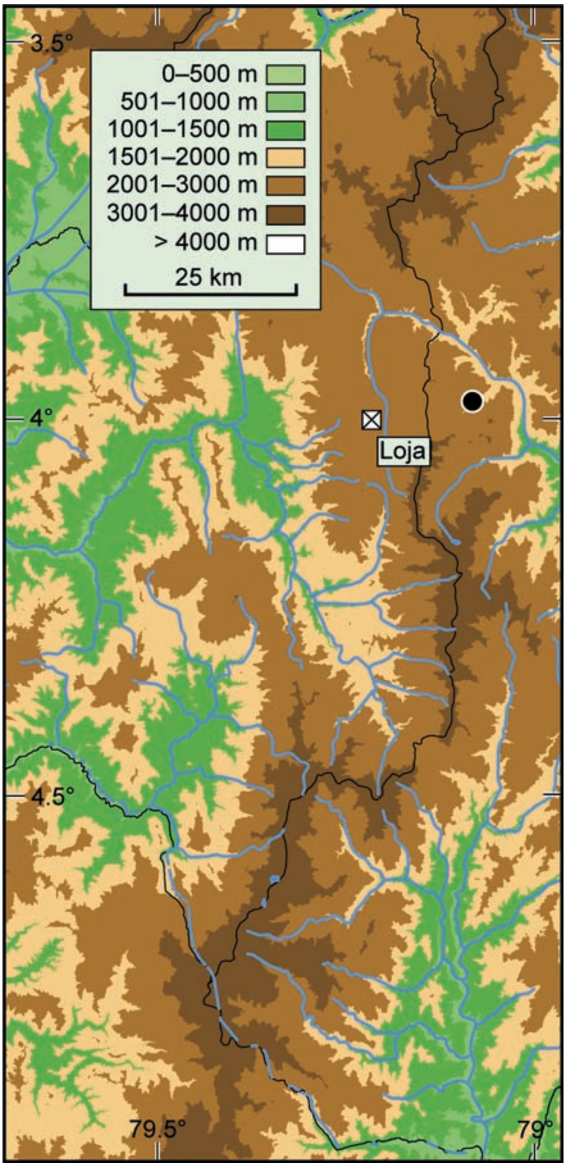

Fig. 12.50 Andean region of southern Ecuador and northern Peru, showing the locality of known occurrences of *Gastrotheca psychrophila*.

an affinity for"; the name was used in allusion to the cold climate at the type locality (Duellman, 1974a).

Remarks

Duellman and Hillis (1987) reported three convergent electromorphs in *Gastrotheca psychrophila* and *G. pseustes*, which otherwise are quite distinct allozymically, and they postulated a possible past hybridization between the two species. Phylogenetic analyses of molecular data (e.g., Wiens et al., 2007; Blackburn and Duellman, 2013) placed *G. psychrophila* with Peruvian taxa (*G. peruana* and *G. stictopleura*).

Gastrotheca (*Gastrotheca*) *rebeccae* Duellman and Trueb

Gastrotheca rebeccae Duellman and Trueb, 1988:172.—Holotype: KU 196800 from Yuraccyacu, on the Tambo–Valle del Apurimac trail, 2620 m (12°47′ S, 73°3′ W), Región de Ayacucho, Peru.

Diagnosis

This moderately small species attain a maximum snout–vent length of 45.7 mm. The tibia length is less than 55% of the snout–vent length, and is slightly longer than the foot. The interorbital distance is noticeably greater than the width of the upper eyelid. The skin on the dorsum usually is smooth or granular, not co-ossified with skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is shorter than the second; the fingers have discs that are much wider than the digit proximal to the disc. The fingers are unwebbed; on the foot the webbing extends maximally to the antepenultimate subarticular tubercle on the fourth toe and the penultimate subarticular tubercle on the third toe. The dorsum is green to tan, usually with a darker middorsal blotch. Markings on the head usually consist of a pale labial stripe, and a dark canthal stripe and interocular bar. A pale dorsolateral stripe is present. The flanks are gray, with or without pale spots; the venter is cream, with or without dark flecks.

Gastrotheca rebeccae is most like *G. excubitor*, *griswoldi*, and *pacchamama* in size and general structure. It is like *G. pacchamama* in having an acutely rounded snout in dorsal view, but unlike that species in having a bluntly rounded snout in profile that barely protrudes beyond the margin of the lower lip, as opposed to a strongly projecting snout in *G. pacchamama*. Moreover, the dorsum of *G. pacchamama* usually lacks a dark mark, whereas a middorsal dark mark is present in most *G. rebeccae*. Also, the hind limb is proportionately longer in *G. rebeccae* than in *G. pacchamama*. The relative width of the interorbital distance to the width of the eyelid differs in the four species: mean values of the percentage of interorbital distance to width of the upper eyelid are *G. excubitor*, 189%; *G. rebeccae*, 150%; *G. pacchamama*, 125%; and *G. griswoldi*, 117%. *G. griswoldi* differs from all of these other species by having proportionately shorter legs; the tibia length is only about 43% of the snout–vent length, and is slightly less than the foot length (44% of snout–vent length). *G. ochoai* is superficially similar to *G. rebeccae*, but *G. ochoai* is smaller (males to 30.4 mm, females to 37.5 mm), and has tubercular skin on the dorsum.

Description

The following description is based on 149 specimens. The body is moderately robust. The maximum snout–vent length is 44.7 mm in males, and 45.7 mm in females. The head is slightly wider than long, and about as wide as the body. The snout is acutely rounded in dorsal view, and is bluntly rounded in profile, barely protruding beyond the anterior margin of the lower jaw. The canthus rostralis is angular in cross-section. The loreal region is slightly concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 150% of the width of the upper eyelid. The internarial area is flat. The nostrils are not protuberant, and are directed laterally at the level of the anterior terminus of the canthus rostralis and at the level of the anterior margin of the lower jaw. The diameter of the eye is equal to or slightly less than its distance from the nostril. The tympanum is vertically ovoid, and is separated from the eye by a distance nearly twice the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is moderately heavy and tubercular, and extends from the posterior corner of the orbit to a point above the insertion of the arm; the fold obscures the upper part of the tympanum.

The arm is moderately slender; ulnar tubercles are absent. The hand is small. The fingers are moderately long, slender, unwebbed, and bear moderately large round discs; the width of the disc on the third finger is slightly greater than the length of the tympanum. The relative lengths of the fingers are I < II < IV < III. The subarticular tubercles are large and round. The supernumerary tubercles are large, round, and present only on the proximal segments. The palmar tubercle is ovoid and elevated; the prepollical tubercle is elliptical and elevated; brown nuptial excrescences are present in breeding males. The hind limb is moderately slender. The tibia length is about 51% of the snout–vent length;

the foot length is about 47% of the snout–vent length. A calcar and tarsal folds are absent; there are numerous small round tubercles on the tarsus. The outer metatarsal tubercle is small and subconical; the inner metatarsal tubercle is small, ovoid, elevated, and barely visible from above. The toes are moderately long. The relative lengths of the toes are I < II < III < V < IV. Webbing is absent between Toes I and II; the webbing formula for the other toes is **II**2—3**III**(2$^+$–2½)—(3–4)**IV**(3–4)—(2–3)**V**. The subarticular tubercles are moderately large and round; the supernumerary tubercles are large, round, and present only on the proximal segments.

The skin on the dorsum is smooth (53%), granular (45%), or pustular (2%); the skin on the flanks is areolate; the skin on the throat, chest, belly, and proximal posteroventral surfaces of the thighs is coarsely granular; the other surfaces are smooth. A pair of tubercles is present below the cloacal opening. The opening of the brood pouch is U-shaped, with its anterior terminus just posterior to the sacrum. The dentigerous processes of the vomers are inclined posteromedially, and are narrowly separated medially between the posterior margins of the moderately large round choanae. Each process bears four to six teeth.

COLOR IN PRESERVATIVE

The dorsum of the body is pale brown or gray, either without dark markings (7%) or with darker markings consisting of an interorbital bar (93%), paravertebral longitudinal marks (9%), broad middorsal mark (54%), or narrow middorsal mark (30%) (Fig. 12.51). The dorsal surfaces of the limbs are uniformly pale brown or gray (9%), or have darker transverse marks (91%). The anterior and posterior surfaces of the thighs are uniformly pale brown or gray (27%) or have dark flecks (73%). A pale labial stripe is present in 73% of the specimens; a pale supracloacal stripe is present in 51%. A dark brown canthal stripe bordered above by a narrow cream line is present in 72% of the specimens. The tympanic region is dark brown; the flanks are either uniformly pale brown or gray (56%), or have dark flecks (19%) or spots (25%). The venter is uniformly cream (51%) or flecked with gray or black (49%).

COLOR IN LIFE

KU 163302–3 from 7.5 km SW Cano, 2970 m, Región de Ayacucho, Peru.—When these frogs were collected, the dorsum was olive green. At night the color changed to tan. The side of the head was coppery brown; the labial stripe was bronze. The axilla, groin, and hidden surfaces of the hind limbs were dull green; the venter was creamy white. The iris was reddish bronze, with black reticulations (Fig. 12.52.A) (W. E. Duellman field notes, 22 February 1975).

Color photos of three recently collected males from Chiquintirca, 2880 m, Región de Ayacucho,

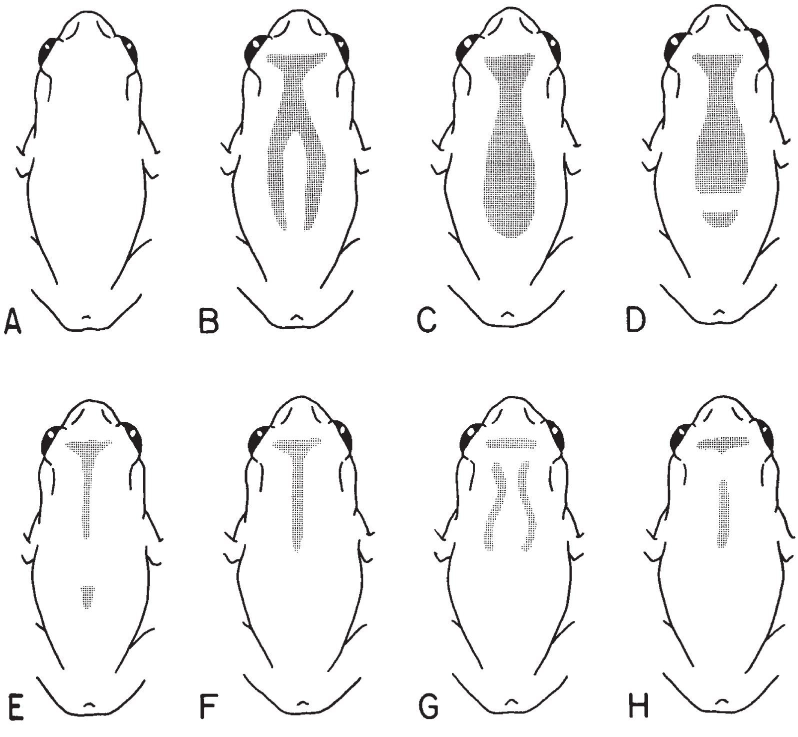

Fig. 12.51 Diagrammatic representative types of the dorsal color patterns in 149 individuals of *Gastrotheca rebeccae*. Pattern A = 11 individuals; Pattern B = 9; Pattern C = 77; Pattern D = 4; Pattern E = 1; Pattern F = 30; Pattern G = 4, Pattern H = 13.

Peru, reveal a dorsal ground color of reddish tan, a noticeably darker reddish-brown middorsal mark, and a bluish-green coloration in the axilla and groin and on the posterior surfaces of the thighs. The venter is dull creamy tan. The iris is deep reddish bronze, with black reticulations (Fig. 12.52B).

MEASUREMENTS

Females are slightly larger than males. Significant differences (ANOVA, $P < 0.01$) between the sexes exist in snout–vent length, head length, and nostril–jaw distance (Table 12.17).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous semicoarse pattern of shallow pits and low rounded ridges. The nasals articulate medially, and are synostotically united; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals are completely articulated medially, and have a narrow supraorbital flange and a small otic flange. A temporal arcade is absent. The frontoparietal does not cover the epiotic eminences; the carotid canal is partially open, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for more than three-fourths the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is long. The postorbital process of the maxilla is massive, and has a broad horizontal articulation with the wide zygomatic process of the squamosal. The head of the squamosal has a narrow crest; the narrow otic plate articulates marginally with the crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in size, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are moderately separated medially, and bear a low irregular ridge ventrally. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a long blunt process on the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located between the posterior quadrants of the choanae.

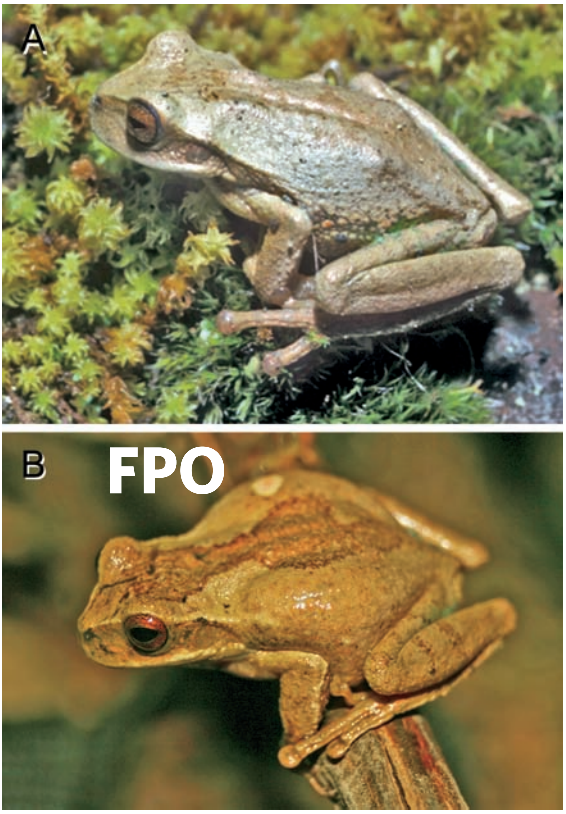

Fig. 12.52 *Gastrotheca rebeccae*. A: KU 163302, male, 30.9 mm SVL, 7.5 km SW Cano, 2970 m, Ayacucho, Peru. B: CORBIDI 6958, male, 32.1 mm SVL, Chicintirca, 2880 m, Ayacucho, Peru. Photos by W. E. Duellman (A) and G. Chávez (B), KUDA.

Life History

No brooding females are known, but the size and number of ovarian eggs are indicative of direct development. One female with a snout–vent length of 44.2 mm, collected at Ccarpa on 15 May 1971, contained 22 eggs, each about 4.5 mm in diameter. Four males with snout–vent lengths of 31.9–32.3 mm were calling 30–40 cm above the ground in dense bushes in humid montane forest. The smallest juvenile (snout–vent length of 17.1 mm) was found on 22 February 1975.

Advertisement Call

The call has not been described.

Distribution and Ecology

Gastrotheca rebeccae occurs at elevations of 2470–2970 m on the eastern slopes of the Cordillera Oriental

Table 12.25 Comparison of color patterns in three populations of *Gastrotheca rebeccae* (numbers are percentages)

Character	Cano (*n* = 2)	Ccarpa-Yanamonte (*n* = 111)	Mitupucuru Yuraccya (*n* = 36)
Canthal stripe	100	84	64
Supratympanic stripe	100	76	81
Labial stripe	100	84	64
Supracloacal stripe	100	—	100
Venter flecked	50	57	25
Dorsal pattern*			
A	50	9	—
B	—	5	8
C	—	53	50
D	—	1	8
E	—	1	—
F	50	15	34
G	—	4	—
H	—	12	—
Flank pattern			
Plain	100	40	39
Dark flecks	—	33	33
Dark spots	—	27	28

*See Fig. 12.53.

that are drained by tributaries of Río Apurimac, in Departamento de Ayacucho in central Peru (Fig. 12.27). Individuals have been found beneath stones in cloud forest by day and on low bushes at night.

Conservation Status

This species categorized as Data Deficient in the IUCN Red List.

Etymology

The specific name *rebeccae* is a patronym for Rebecca A. Pyles, who, as a University of Kansas graduate student, applied her knowledge of multivariate analytical methods and computational techniques to research on *Gastrotheca* (Duellman and Trueb, 1988).

Remarks

This highly variable species originally was confused with *Gastrotheca pacchamama*, from which it differs not only in color pattern and some external features, but also in several cranial characters: robustness of the crista parotica, separation of the frontoparietals, degree of separation of the palatines, and shapes of the vomers (Duellman and Trueb, 1988, their Fig. 15).

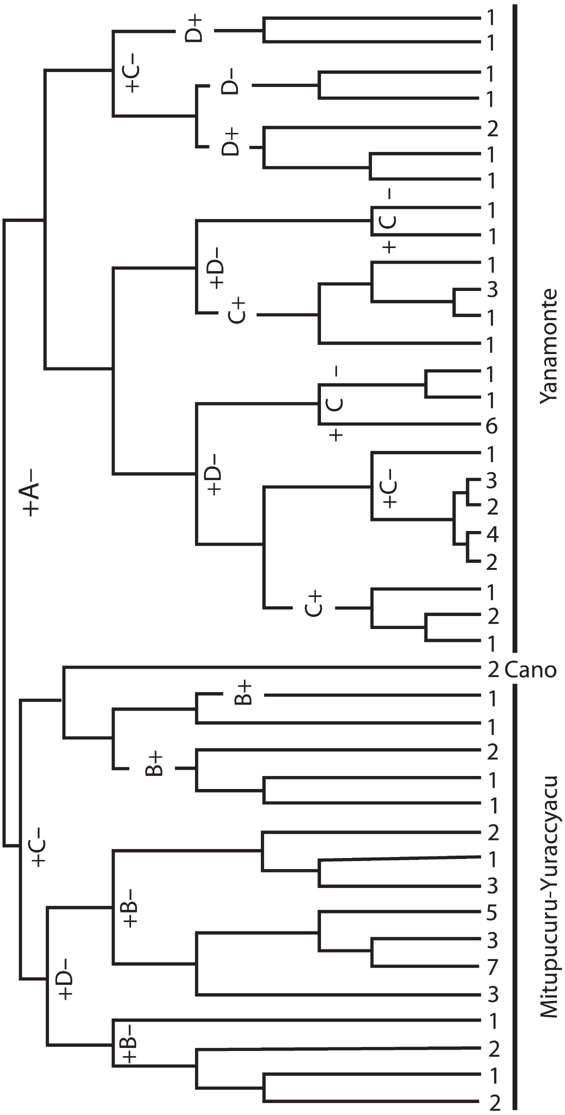

Fig. 12.53 Phenogram, based on a cluster analysis of color pattern characteristics in three populations of *Gastrotheca rebeccae*: from Cano (*n* = 2), from Mitupucuru-Yuraccyacu (*n* = 36), and from Yanamonte (*n* = 40). Numbers at the ends of the horizontal lines = number of specimens. Letters on the vertical lines indicate major dichotomies (+ = presence, − = absence): A = supracloacal stripe; B = intrusion of the dorsal color onto the flank; C = pattern on the posterior surface of the thigh; D = pattern on the belly.

Although the localities from which this species are known are in close geographic proximity, there are differences of 500 m in elevation. A comparison of samples from high (2970 m at Cano), intermediate (2800 m at Yanamonte), and low (2470–2680 m at Ccarpa, Mitupucuru, and Yuraccyacu) elevations revealed some consistent differences in color patterns. These are illustrated (Fig. 12.51) and coded (Table 12.25). A cluster analysis showed that the samples from each of the three areas maintained their integrity (Fig. 12.53). A second cluster analysis of character states of skin texture and foot webbing reveals that the samples from Cano and Yanamonte are alike in having smooth skin.

Gastrotheca (*Gastrotheca*) *splendens* (Schmidt)

Hyla splendens Schmidt, 1857:11.—Holotype: ZMJU 1800 from "Chiriqui-Flusse unweit Bocca del Toro, Panama" [in error; perhaps Bolivia].
Gastrotheca splendens—Duellman, 1977:19.

Diagnosis

In this medium-sized species, the maximum known snout–vent length is 51.3 mm. The tibia length is less than 50% of the snout–vent length, and is slightly longer than the foot. The interorbital distance is less than twice the width of the upper eyelid. The skin on the dorsum is smooth, co-ossified with the dorsal surfaces of the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first finger is shorter than the second; the discs on the fingers are slightly wider than the digits proximal to the discs. The outer fingers are about one-third webbed; on the foot the webbing extends nearly to the antepenultimate subarticular tubercle on the fourth toe and a point between antepenultimate and penultimate subarticular tubercles on the fifth toe. The dorsum is pale brown, with numerous dark brown spots. Markings on the head consist of dark brown spots on the edges of the upper lips, and diffuse dark brown spots on the canthus rostralis. A pale dorsolateral stripe is absent. The flanks are creamy brown, with dark brown spots; the venter is cream, with brown flecks peripherally on the chin.

In color pattern *Gastrotheca splendens* superficially resembles *G. marsupiata*, a smaller species that lacks both webbing between the outer fingers and cranial co-ossification. Other species that have cranial co-ossification differ from *G. splendens* in significant ways. For example, in *G. galeata* the skull is spatulate, and the maxillae and premaxillae are flared; in *G. trachyceps* co-ossification is restricted to the loreal and postorbital regions. All of the dorsal roofing bones of the skull are co-ossified with the overlying skin in *G. fissipes*, *megacephala*, *prasina*, and *recava*. In *G. nicefori* and *G. ovifera*, a distinct transverse occipital crest is present, and in the latter species the crest bears dorsal projections.

Description

The following description is based on two specimens. The body is moderately robust. The snout–vent length is 53.1 mm in a male, and 44.7 mm in a female. The head is slightly wider than long, but not as wide as the body. The snout is bluntly rounded in dorsal view and in profile (Fig. 12.54). The canthus rostralis is almost angular in cross-section. The loreal region is concave; the lips are slightly flared. The top of the head is flat. The lateral edges of the frontoparietals are slightly elevated. The interorbital distance is about 165% of the width of the upper eyelid. The internarial area is slightly concave. The nostrils are barely protuberant, and are directed laterally at a level slightly posterior to the anterior margin of the lower jaw. The diameter of the eye is about equal to its distance from the nostril. The tympanum is round, and is separated from the eye by a distance half again the length of the tympanum. The tympanic annulus is distinct and smooth. The supratympanic fold is weak, does not extend onto the flank, and barely covers the posterodorsal edge of the tympanum.

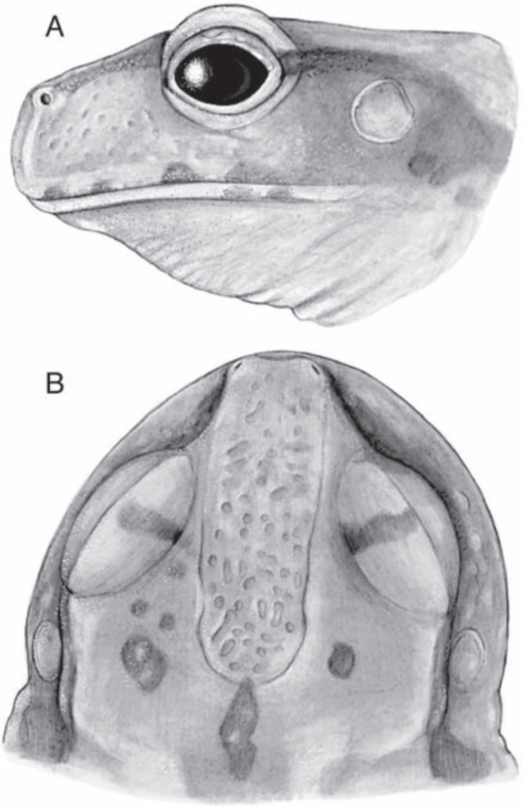

Fig. 12.54 Head of *Gastrotheca splendens* (MNK 1988). A: lateral view. B: dorsal view. Drawings by J. B. Pramuk.

The arm is moderately slender, and lacks ulnar tubercles. The hand is moderately large. The fingers are long, and bear small round discs; the width of the disc on the third finger is slightly less than the length of the tympanum. The relative lengths of the fingers are I < II < IV < III. The first and second fingers are unwebbed; the webbing formula for the outer fingers is **III**2—2½**IV**. Lateral fringes are absent on the digits. The subarticular tubercles are small and round; none are bifid. The supernumerary tubercles are small, indistinct, and present only on the proximal segments. The palmar tubercle is small, low, and weakly bifid; the prepollical tubercle is low and elongate; the condition of the nuptial excrescences is unknown. The hind limb is moderately slender. The tibia length is about 46% of the snout–vent length; the foot length is 42% of the snout–vent length. Calcars, heel tubercles, tarsal folds, and an outer metatarsal tubercle are absent. The inner metatarsal tubercle is low, ovoid, and not visible from above. The toes are moderately long, and have terminal discs that are slightly smaller than those on the fingers. The relative lengths of the toes are I < II < III = V < IV. The toes are less than one-half webbed; the webbing formula is **I**2^+—3^-**II**3^-—2½**III**2½—3^+**IV**3^+—2½**V**. The subarticular tubercles are small and round; the supernumerary tubercles are indistinct, and are present only on the proximal segments.

The skin on the head is co-ossified with the maxillae, nasals, frontoparietals, and anterior rami of the squamosals; the skin on the dorsum and flanks is smooth; the skin on the belly and proximal posteroventral surfaces of the thighs is weakly granular; the other ventral surfaces are smooth. The opening of the brood pouch is broadly U-shaped, with the anterior border posterior to the level of the sacrum. The dentigerous processes of the vomers are slightly inclined posteromedially, and are narrowly separated medially. Each process bears five to seven teeth.

COLOR IN PRESERVATIVE

The dorsum is dull grayish brown or tan, with dark brown markings consisting of small to large irregular spots on the dorsum of the body (Fig. 12.55). The markings on the limbs are arranged diagonally: four rows on the thighs and shanks, three rows on the foot, and two on the forearm. The flanks are slightly paler than the dorsum, and have irregular brown spots, with or without pale centers. The side of the head is brown, with small irregular dark brown spots on the upper lip, as well as diffuse dark spots along the canthus that do not form a distinct canthal stripe. The tympanum is tan. The tympanic annulus is tan or dark brown. The venter is creamy white, with or without dark brown flecks along the margin of the lip and laterally on the chest and belly. The anterior and posterior surfaces of the thighs and the axilla and groin are creamy tan.

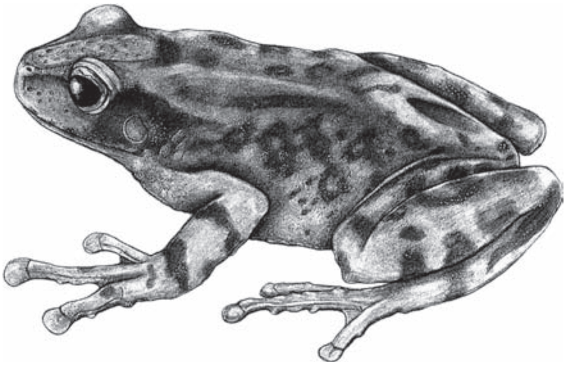

Fig. 12.55 *Gastrotheca splendens* (MNK 1988), female, 44.7 mm SVL, Abra de la Cruz, Parque Nacional Amboró, Santa Cruz, Bolivia. Drawing by J. B. Pramuk.

COLOR IN LIFE

Unknown.

MEASUREMENTS

Data (in mm) are for a female (MNK 1988), followed in parentheses with measurements for a male (ZMJU 1800) when available: snout–vent length 44.7 (51.3), tibia length 19.9 (25.6), foot length 18.4 (22.0), head length 14.6 (16.1), head width 15.5 (18.6), interorbital distance 4.3 (6.4), upper eyelid width 2.6, internarial distance 2.6, eye diameter 3.8, eye–nostril distance 4.3, and tympanum diameter 2.3. Presumably, females of this species grow to be larger than males, as in other species of *Gastrotheca*.

CRANIAL OSTEOLOGY

No skeletal preparations are available. From an external examination, the nasals, sphenethmoid, frontoparietal, maxillae, and crests of the squamosals are co-ossified with the overlying skin, and the sphenethmoid is sculptured.

Life History

The absence of brooding females or tadpoles precludes any knowledge of development. If this species is like other *Gastrotheca* inhabiting cloud forest, *G. splendens* probably has eggs that hatch as froglets.

Advertisement Call

Unknown.

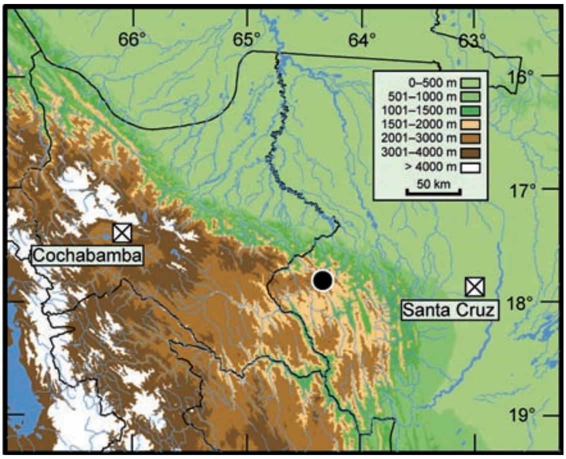

Fig. 12.56 Central Bolivia, showing the locality of the known occurrence of *Gastrotheca splendens*.

Distribution and Ecology

Gastrotheca splendens is known from only one locality, at an elevation of 2286 m in cloud forest on the eastern slopes of the Andes in central Bolivia (Fig. 12.56).

Conservation Status

In the IUCN Red List, *Gastrotheca splendens* is categorized as Endangered, because it is known from only one locality, in the Parque Nacional Amboro in Departamento de Santa Cruz, Bolivia.

Etymology

The specific name is from the Latin *splendidus*, meaning "bright" or "splendid."

Remarks

In the mid-1800s, Polish botanist Josef Warszewicz collected in Central America and western South America (Colombia, Peru, and Bolivia). Amphibians and reptiles that he collected were reported on by Schmidt (1857, 1858), who described several new taxa. Some of the material collected by Warszewicz was mislabeled by the time the specimens were examined by Schmidt. As pointed out by Savage (1970), some species supposedly from Chiriquí and Veraguas in Panama have never been found subsequently in Central America. One of these is *Hyla splendens*, purportedly from Chiriquí, Panama. The name was associated with *Hyla* until Duellman (1977) examined the holotype, placed the species in *Gastrotheca*, and noted that possibly it was from Bolivia. The only other specimen of *G. splendens* was collected in 1996 and reported on by Duellman and De la Riva (1999).

Gastrotheca (*Gastrotheca*) *stictopleura* Duellman, Lehr, and Aguilar

Gastrotheca stictopleura Duellman, Lehr, and Aguilar, 2001: 2.—Holotype: MUSM 20319 from Tranca Grande at Chaglla, Provincia de Pachitea, Región de Huánuco, Peru.

Diagnosis

Females of this moderately large species attain a snout–vent length of 68.3 mm. The tibia length is about 49% of the snout–vent length, and is noticeably shorter than the foot. The interorbital distance is noticeably greater (160%) than the width of the upper eyelid. The skin on the dorsum is finely shagreen, not co-ossified with the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or pronounced tubercles. The tympanic annulus is smooth. The first finger is shorter than the second; the fingers bear discs that are much wider than the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends to the penultimate subarticular tubercle on the fourth toe and the distal subarticular tubercle on the fifth toe. The dorsum is nearly uniformly green. Markings on the head consist of pale labial and canthal stripes, with the latter bordered below by brown. A white dorsolateral stripe is present, and is bordered below by brown. The flanks are green, with small white spots posteriorly; the venter is creamy tan.

Superficially, *Gastrotheca stictopleura* is most like *G. lateonota* and *G. monticola*; all three species are similar in size and most proportions, but there are some significant morphometric differences among the species. *G. stictopleura* has a significantly larger head than *G. lateonota*. In profile, the snout of *G. stictopleura* is more gradually inclined anteroventrally than in *G. monticola*; the snout is truncate in *G. lateonota*. The ventral color pattern is different in the three species: the belly is dull grayish brown in *G. lateonota*, cream with black spots in *G. monticola*, and creamy tan with a few brown flecks in *G. stictopleura*. *G. dysprosita* has a bluntly rounded snout in profile; it also differs from *G. stictopleura* by having a green dorsum with a narrow yellow middorsal stripe, and green flanks with small yellow spots. Furthermore, *G. dysprosita* lacks a dark canthal stripe and pale labial stripe. In *G. lateonota* and *G. stictopleura*, the squamosals lack a median flange, and are not in contact with the otic flanges of the frontoparietals; these two bones are in contact and form a complete temporal arcade in *G. dysprosita* and *G. monticola*.

Description

The following description is based on three specimens. The body is robust. The maximum known snout–vent length is 68.3 mm in females; males are unknown. The head is slightly wider than long, and narrower than the body. The snout is moderately long, acutely rounded in dorsal view, and inclined anteroventrally in profile. The canthus rostralis is rounded in cross-section. The loreal region is noticeably concave; the lips are rounded. The top of the head is slightly concave. The interorbital distance is about 160% of the width of the upper eyelid. The internarial area is slightly concave. The nostrils are slightly protuberant anterolaterally at a point well behind the anterior margin of the lower jaw. The diameter of the eye is equal to its distance from the nostril. The tympanum is vertically ovoid, and is separated from the eye by a distance about half again the length of the tympanum. The tympanic annulus is smooth, and is distinct anteriorly and ventrally. The supratympanic is fold moderately weak, barely overlaps the upper edge of the tympanum, and extends from the posterior corner of the orbit to a point above the insertion of the arm.

The arm is moderately robust, and lacks ulnar tubercles. The hand is moderately large. The fingers are unwebbed, but distinct lateral fringes are present on all of the digits except the thumb. The discs are moderately large, and have a median longitudinal groove in the anterior part of each pad; the width of the disc on the third finger is noticeably greater than the length of the tympanum. The relative lengths of the fingers are I < II < IV < III. The subarticular tubercles are large and rounded; none are bifid. Supernumerary tubercles are absent. The palmar tubercle is low and elliptical; the prepollical tubercle is elongately elliptical; the condition of the nuptial excrescences is unknown. The hind limb is moderately robust. The tibia length is about 50% of the snout–vent length; the foot length is about 45% of the snout–vent length. Calcars, heel tubercles, and an outer tarsal fold are absent. The inner tarsal fold is distinct, and extends the full length of the tarsus. An outer metatarsal tubercle is absent; the inner metatarsal tubercle is ovoid, and is barely visible from above. The toes are long and slender, and bear distinct lateral fringes. The relative lengths of the toes are I < II < III < V < IV. The toes are less than one-half webbed; the webbing formula is **I**2—2**II**1—3**III**2—3**IV**3—2^{-}**V**. The discs are slightly smaller than those on the fingers. The subarticular tubercles are prominent and round; the supernumerary tubercles are prominent, and are present only on the proximal segments.

The skin on the dorsum is shagreen; the skin on the ventral surfaces of the forearms and shanks is smooth; the other ventral surfaces are granular. Vertical cloacal folds are present. There is a transverse row of four rounded tubercles on the posterior surface of each thigh, lateral to the cloaca; the tubercles decrease in size distally. The opening of the brood pouch is U-shaped, with the apex just posterior to the sacrum. The dentigerous processes of the vomers are slightly oblique posteromedially, and are narrowly separated medially at the level of the posterior margins of the moderately large and nearly round choanae. Each process bears five or six teeth.

COLOR IN PRESERVATIVE

The dorsal surfaces of the head, body, and limbs are bluish gray, either without markings (67%) or with faint tan markings (33%) consisting of an elongate X-shaped mark on the body extending from the upper eyelids to the sacrum, a short longitudinal middorsal mark posterior to the sacrum, and irregular marks on the dorsal surfaces of the limbs. A narrow cream dorsolateral stripe originates as a vertical line on the snout, passes along the canthus rostralis, margin of the upper eyelid, and supratympanic fold, and terminates on the upper flank at about midlength of the body; this stripe is bordered below by a brown stripe. A narrow cream labial stripe is present. The flanks are green (67%) or brown (33%). The groin is green with white spots (67%), or pale tan with vertical brown bars (33%). A narrow transverse white stripe is present above the vent. The crests of the vertical folds and tubercles lateral to the vent are white. There is a narrow white ventrolateral stripe on the forearm, and a transverse white bar on the heel. The dorsal surfaces of the fingers and innermost three toes are tan; the other toes and all discs are bluish gray. The throat is pale bluish gray, with creamy white granules; other ventral surfaces and the anterior and posterior surfaces of the thighs are dull creamy tan, with brown flecks on the belly.

COLOR IN LIFE

The dorsum is predominately green; the venter is tan (Fig. 12.57).

MUSM 20319.—In this adult female, the dorsal surfaces of the head, body, and limbs and the loreal and tympanic regions are bright dark green, with diffuse salmon markings on the body and limbs. The labial and dorsolateral stripes are cream; the dorsolateral stripe is bordered below by brown. The spots on the flanks and lateral to the vent are white. The throat,

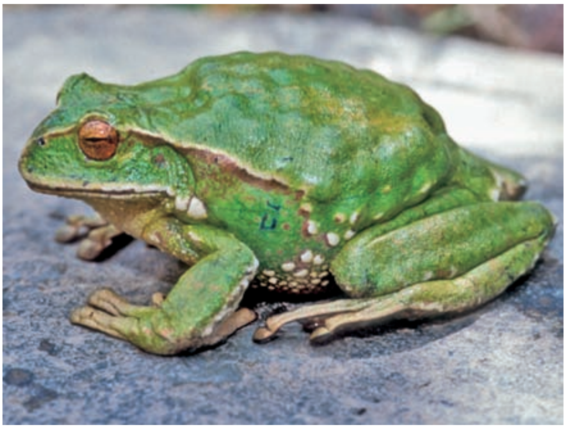

Fig. 12.57 *Gastrotheca stictopleura* (MUSM 20319, holotype), female, 68.3 mm SVL, Chaglla, Huánuco, Peru. Photo with permission granted by the photographer, E. Lehr. Copyright 1998. All rights reserved.

chest, and ventral surfaces of the forelimbs are cream to yellow, with diffuse green and salmon spots. The belly is pale brown. The ventral surfaces of the shanks are green; the palmar and plantar surfaces are gray. The iris is metallic orange, with fine black reticulations (E. Lehr field notes, 23 August 1998).

SMF 80328–29.—These two juveniles have a green dorsum, with or without metallic-salmon spots on the head, body, and limbs. The hands and feet are cream. The canthal and dorsolateral stripes are cream, bordered below by brown. The labial stripe is cream. The flanks are white, with dark brown markings. The cloacal region is dark brown, bordered by white. The throat is pale brown; the chest and belly are dark brown, with pale brown spots. The iris is salmon (E. Lehr field notes, 23 August 1998).

MEASUREMENTS

The measurements of the only adult (a female) are snout–vent length 68.3, tibia length 34.1, foot length 30.5, head length 20.3, head width 23.1, interorbital distance 8.0, eyelid width 5.0, internarial distance 4.1, eye diameter 5.8, eye–nostril distance 5.0, orbit–jaw distance 3.0, nostril–jaw distance 5.3, tympanum diameter 3.0, thumb length 12.0, third finger length 21.8, and width of disc on third finger 3.5.

CRANIAL OSTEOLOGY

Partial dissection of the holotype revealed that the dermal roofing bones are not co-ossified with the overlying skin. The squamosal lacks a medial flange, and is not in contact with the otic flange of the frontoparietal.

Life History

Indirect evidence indicates that *Gastrotheca stictopleura* produces tadpoles that complete their development in ponds, but tadpoles are unknown. The only brooding female (the holotype) contained an estimated 82 eggs in the brood pouch (Duellman et al., 2001); these eggs are each about 5.3 mm in diameter and are in developmental stages 17–20. The number and size of the eggs indicate that eggs of this species hatch as tadpoles.

The brooding female was found in August, as were two juveniles having snout–vent lengths of 28.5 and 32.7 mm.

Advertisement Call

Males are unknown; no calls were heard at the type locality.

Distribution and Ecology

This species is known from elevations of 2500–3090 m in humid subpáramo and humid montane forest in the regions of Huánuco and Pasco in central Peru (Fig. 12.58). All specimens were obtained by local residents, who claimed that the frogs were found in trees. The only other species of *Gastrotheca* at the type locality is *G. griswoldi*, a smaller terrestrial species in which eggs hatch as froglets.

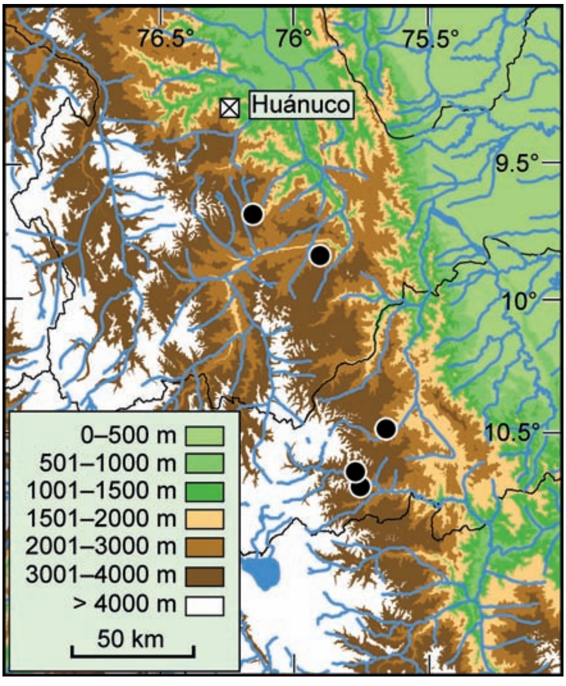

Fig. 12.58 Central Peruvian Andean region, showing the localities of known occurrences of *Gastrotheca stictopleura*.

Conservation Status

In the IUCN Red List, *Gastrotheca stictopleura* is categorized as Endangered, because of its limited range in an area of excessive deforestation for agricultural purposes.

Etymology

The specific name is derived from the Greek *stiktos*, meaning "dappled" or "spotted," and the Greek *pleura*, meaning "side"; the name refers to the spotted pattern on the flanks (Duellman et al., 2001).

Remarks

Duellman et al. (2001) considered *Gastrotheca stictopleura* to be most closely related to *G. lateonota*, but genomic data place those species in different clades.

Gastrotheca (*Gastrotheca*) *testudinea* (Jiménez de la Espada)

Nototrema testudineum Jiménez de la Espada, 1871:62.—Holotype: MNCN 155 from San José de Moti, Provincia de Napo, Ecuador.

Nototrema viviparum Andersson, 1945:82.—Syntypes: NHRM 1964 (10 specimens) from Baños, Cerro Tungurahua, and Río Pastaza watershed, Ecuador. Synonymy fide Duellman, 1974b:4.

Gastrotheca testudineum—Peters, 1955:348.

Gastrotheca testudinea—Duellman, 1974b:4.

Gastrotheca (*Opisthodelphys*) *testudinea*—Dubois, 1987: 31.

Diagnosis

This large species attains a snout–vent length of 82.6 mm. The tibia length is less than 60% of the snout–vent length, and is longer than the foot. The interorbital distance is about twice the width of the upper eyelid. The skin on the dorsum is areolate, adherent to the skull, and lacks transverse ridges. Supraciliary processes are absent. The heel usually bears a tubercle. The tympanic annulus is granular. The first finger is longer than the second; the discs on the fingers are much wider than the digits proximal to the discs. The fingers are unwebbed; on the foot the webbing extends maximally to a point midway between the antepenultimate and penultimate subarticular tubercles of the fourth toe and a point midway between the penultimate and distal subarticular tubercles of the fifth toe. The dorsum is tan, usually with transverse bars, a narrow middorsal mark, or flecks. Markings on the head usually consist of a pale labial stripe and broad dark interocular bar. A pale dorsolateral stripe is absent. The flanks are tan, with dark vertical bars; the venter is bronze.

Individuals of *Gastrotheca testudinea* that have a narrow middorsal dark mark are patterned like *G. ovifera*, which differs in having the skin co-ossified with the skull and a prominent transverse occipital ridge with dorsal projections. Superficially, *G. andaquiensis* is like *G. testudinea*, but the former has an elongate calcar on the heel and a granular interocular ridge, and it lacks vertical dark bars on the flanks.

Description

The following description is based on 47 specimens. The body is robust. The maximum snout–vent length is 61.1 mm in males, and 82.6 mm in females. The head is slightly wider than long, but not as wide as the body. The snout is rounded in dorsal view, and in profile is inclined from the nostrils to a rounded tip. The canthus rostralis is angular in cross-section. The loreal region is concave; the lips are slightly flared. The top of the head is flat. The interorbital distance is about 200% of the width of the upper eyelid. The internarial area is flat to slightly convex. The nostrils are slightly protuberant, and are directed dorsolaterally below the anterior terminus of the canthus rostralis at a point slightly posterior to the anterior margin of the lower lip. The diameter of the eye is slightly less than its distance from the nostril. The tympanum is round, and is separated from the eye by a distance about 1.75 times the length of the tympanum. The tympanic annulus is distinct and tubercular; the heavy supratympanic fold extends onto the flank, and obscures the upper edge of the tympanum.

The arm is moderately robust, and bears a row of low round ulnar tubercles. The hand is moderate in size. The fingers are moderately long, and bear large round discs; the width of the disc on the third finger is much greater than the length of the tympanum. The relative lengths of the fingers are I > II < IV < III. The fingers are unwebbed, but distinct lateral fringes are present on both sides of all digits. The subarticular tubercles are large and round; none are bifid. The supernumerary tubercles are moderately large and round. The palmar tubercle is low and bifid; the prepollical tubercle is elliptical; the thumb bears a brown nuptial excrescence in breeding males. The hind limb is moderately slender. The tibia length is about 54% of the snout–vent length; the foot length is about 47% of the snout–vent length. A small tubercle usually (81%) is present on the heel; a row of low tubercles is evident on the ventral surface of the tarsus. The low inner tarsal fold is only on the distal one-third of the tarsus. The outer metatarsal tubercle is small and subconical; the inner metatarsal tubercle is large, elliptical, and visible from above. The relative lengths of the toes are I < II <

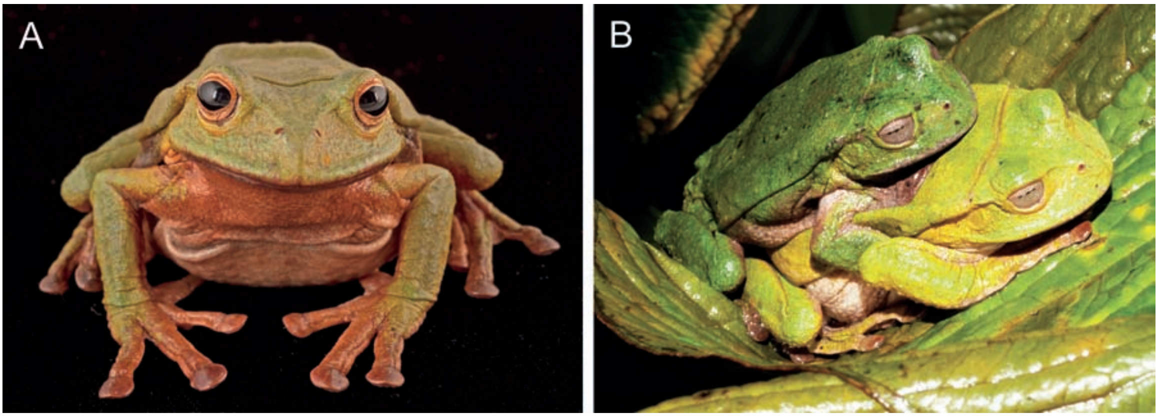

Fig. 12.59 *Gastrotheca testudinea.* A: adult female, showing the pectoral pockets. B: amplectant pair. Both from Zuñac, Morona-Santiago, Ecuador. Photos by L. A. Coloma, KUDA.

III < V < IV. The toes are about one-half webbed; the webbing formula is **I**(2$^-$–2)—(2–2½)**II**(1½–2$^-$)—(2½–3) **III**(1½–2$^-$)—(2½–3)**IV**(2½–3)—(1½–2)**V**. The subarticular tubercles are large and round; the supernumerary tubercles are subconical, and are present only on the proximal segments.

The skin on the dorsum and flanks is areolate; the skin on the belly and posteroventral surfaces of the thighs is coarsely granular; the other ventral surfaces are smooth. In some adults of each sex, folds of skin ventrolaterally in the pectoral region form pockets, with the opening positioned anteriorly (Fig. 12.59A). There are small conical tubercles between the orbit and the tympanum; a pair of tubercles is present below the cloacal opening. The opening of the brood pouch is narrowly U-shaped, with the anterior margin at the level of the sacrum. The dentigerous processes of the vomers are transverse, and are widely separated medially between the posterior margins of the choanae. Each process bears 4–11 teeth.

COLOR IN PRESERVATIVE

The dorsum is tan to gray, with chocolate-brown to reddish-brown markings, including flecks on the side of the head, usually (66%) a broad interocular bar, distinct narrow transverse bars on the limbs, and usually (83%) various markings on body: flecks only (13%), a narrow middorsal mark (30%), or transverse marks (40%). A narrow pale labial stripe usually (91%) is present. The flanks are uniformly tan or gray (15%), or have lateral extensions of the dorsal transverse marks (40%) or vertical black bars (45%). The anterior surfaces of the thighs are tan, usually (98%) with vertical black bars; the posterior surfaces of the thighs are uniformly dark brown to black. A dark patch in the cloacal region usually is not evident. A pale supracloacal stripe usually (74%) is absent, but pale subcloacal spots usually (77%) are present. There is a narrow pale stripe on the heels (66%); the outer toes are colored like the inner ones.

COLOR IN LIFE

Living frogs have many subtle colors that are not evident in preserved specimens (Fig. 12.60). Furthermore, as is evident from the following descriptions, considerable variation obtains within a local sample, and ontogenetic changes occur.

A pair from Zuñac, Morona-Santiago, Ecuador.—The dorsum is uniformly green; the venter is orange to orange tan; the vocal sac in the male is dark brown. The iris is golden tan, with reddish-brown reticulations (Fig. 12.59B).

KU 163270 from Río Kosñipata, 4 km SW Santa Isabel, Región de Cusco, Peru.—The dorsum is olive tan, with one green and four cream spots (Fig. 12.60C). The flanks are yellowish tan, with black venations and a large black spot in the groin. The upper surfaces of the thighs are orange, with gray transverse bars; the posterior surfaces of the thighs are grayish brown, with large black markings. The belly is pinkish bronze; the plantar and palmar surfaces are dark gray. The labial and heel stripes are creamy yellow; the supracloacal stripe is orange. The iris is dull bronze, with fine black reticulations (W. E. Duellman field notes, 10 February 1975).

KU 163271–76 from Tutumbaro, Río Piene, Región de Ayacucho, Peru.—The dorsum is tan, with olive-brown middorsal marks (Fig. 12.60A, B). The transverse bars on the limbs are brown (dark green on the thighs of KU 163272). The flanks, anterior surfaces of the thighs, and ventral surfaces of the shanks and feet are creamy tan, with black spots (flanks tan or cream, with

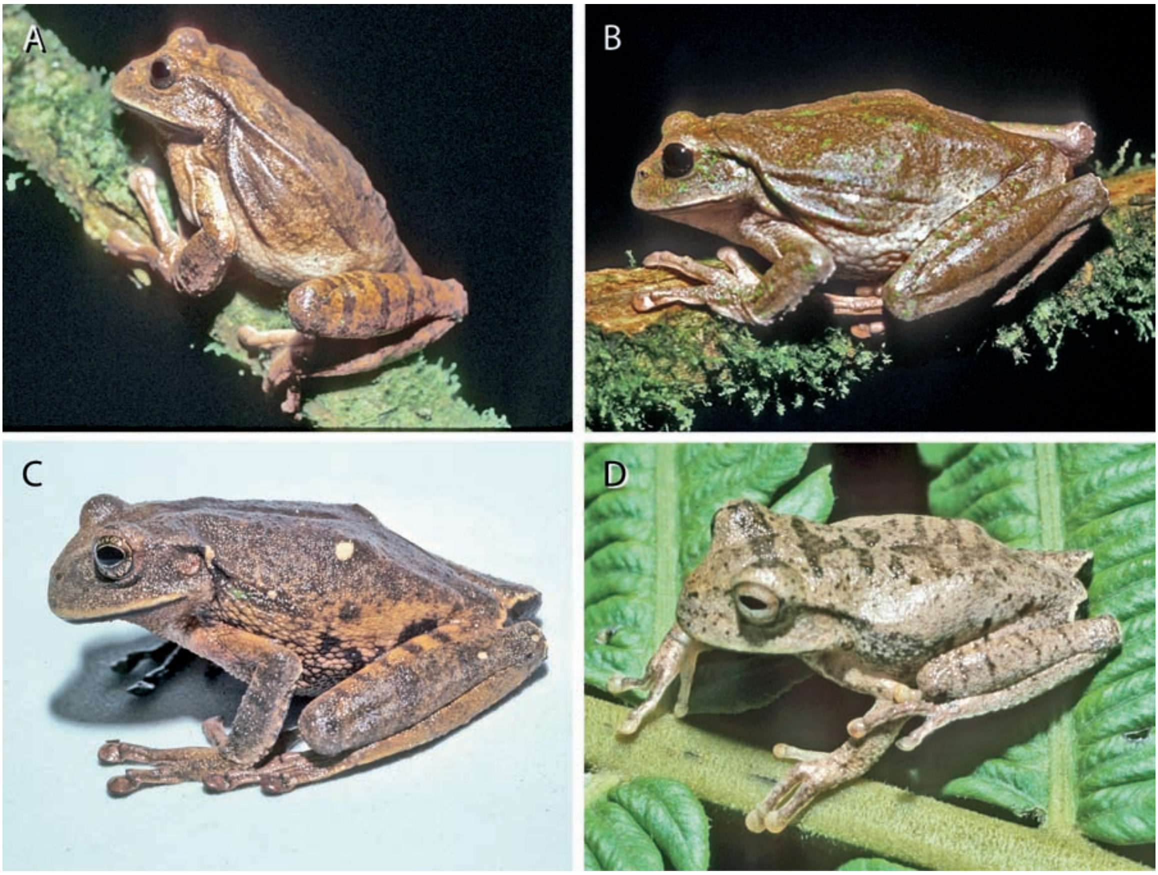

Fig. 12.60 *Gastrotheca testudinea*. A: KU 163274, female, 82.6 mm SVL, Tutumbaro, 1840 m, Ayacucho, Peru. B: KU 163276, female, 59.1 mm SVL, same locality. C: KU 163270, male, 45.2 mm SVL, Río Kosñipata, 4 km SW Santa Isabela, 1740 m, Cusco, Peru. D: KU 212076, juvenile, 19.7 mm SVL, Venceremos, 1630 m, San Martín, Peru. Photos by W. E. Duellman.

blue spots, in KU 163271 and 163273). The labial, ulnar, supracloacal, and heel stripes and subcloacal tubercles are creamy white. The iris is copper, with fine black reticulations. In KU 163272 the post-tympanic region is dark metallic green. The throat is copper; the belly is pale tan, with brown and black flecks. The plantar and palmar surfaces are brownish gray; the dorsal surfaces of the hands and feet and the webbing are metallic tan. The tongue is pink; the buccal lining is pale blue. In KU 163273 the posterior surfaces of the thighs are brown with blue spots. At night the dorsum in KU 163276 was tan with dark brown markings and metallic-green flecks, but by day it was dark brown with cream flecks (W. E. Duellman field notes, 20 February 1975).

CORBIDI 5385 from Ozonampiato, Región de Cusco, Peru.—This adult female has a reddish-brown dorsum, with metallic-green flecks; the flanks are creamy tan. The iris is dark bronze (photo by G. Chavéz, 15 October, 2009).

KU 212076 from Venceremos, Región de San Martín, Peru.—This juvenile has a tan dorsum, with brown markings (Fig. 12.60D). The labial stripe is cream. The anterior and posterior surfaces of the thighs are pale orange; the venter is cream with brown flecks. The iris is creamy bronze (W. E. Duellman field notes, 1 February 1989).

KU 212077 from E slope Abra Pardo Miguel, Región de San Martín, Peru.—This juvenile has a dorsum that is olive green medially, and pinkish tan with black flecks laterally. The limbs are barred pinkish tan and grayish green; the anterior and posterior surfaces of the thighs are orange brown. The venter is creamy yellow, with brown spots. The iris is pinkish silver (W. E. Duellman field notes, 31 January 1989).

KU 202701 from 18.6 km WSW Plan de Milagro, Provincia de Morona-Santiago, Ecuador.—This juvenile has a pale olive-tan dorsum, with minute red tubercles in the occipital region. The suborbital area is dull green; the labial and canthal stripes are cream; the heel stripes and subcloacal tubercles are creamy white.

Table 12.26 Univariate statistics for adults of *Gastrotheca testudinea*

	Males (n = 8)			Females (n = 23)		
Character	Mean	Range	SD	Mean	Range	SD
Snout–vent length**	55.7	49.8–61.1	3.83	65.5	56.8–82.6	8.57†
Tibia length*	30.3	26.6–35.8	3.00	35.5	27.1–46.0	5.28
Foot length**	26.1	23.7–27.7	1.54	30.9	24.2–40.1	4.63†
Head length**	18.8	17.2–20.0	1.15	22.2	18.0–28.0	3.10†
Head width**	22.2	18.7–23.4	1.62	25.7	21.4–32.9	3.30†
Interorbital distance*	7.2	6.3–8.1	0.68	8.6	7.1–12.8	1.61
Eyelid width	3.8	3.0–4.4	0.42	3.8	3.1–5.0	0.87†
Internarial distance**	3.2	2.9–3.4	0.19	4.2	2.8–5.0	0.56†
Eye diameter*	5.3	4.3–6.1	0.57	6.0	4.5–7.5	0.75
Eye–nostril distance**	5.1	4.5–6.1	0.52	5.9	4.8–7.5	0.79
Orbit–jaw distance**	2.9	2.5–3.2	0.25	3.6	2.6–5.0	0.67†
Nostril–jaw distance**	4.2	3.7–4.5	0.29	4.9	3.7–6.3	0.70†
Tympanum diameter**	2.5	2.0–2.9	0.28	3.0	2.3–4.4	0.63†
Thumb length**	10.2	9.4–10.8	0.66	12.2	9.8–16.8	2.09†
Third finger length**	19.4	16.7–21.6	1.51	23.0	18.7–31.1	3.45†
Disc width*	3.6	2.8–4.1	0.45	4.1	3.4–5.3	0.56

*Differences between the means of the sexes are significant (ANOVA, $P = 0.05$).

**Differences between the means of the sexes are significant (ANOVA, $P \leq 0.01$).

†Variances are non-homogeneous (Brown-Forsythe test, $P \leq 0.05$).

The venter is pale gray; the posterior surfaces of the thighs and groin are dark blue, with orange spots in the latter. The iris is bronze, with black reticulations (W. E. Duellman field notes, 4 March 1984).

MEASUREMENTS

In most measurements females are significantly larger than males, but the variances of many measurements are non-homogeneous (Table 12.26).

CRANIAL OSTEOLOGY

The sphenethmoid, along with the skull table, is sculptured in a homogeneous semicoarse pattern of shallow pits and low rounded ridges. The nasals articulate medially, but are not fused to one another; their borders are distinct from the sphenethmoid; posterolaterally, the nasal articulates with the anterolateral margin of the frontoparietal. The frontoparietals are completely articulated medially, and have a wide supraorbital flange and a moderate-sized otic flange. A temporal arcade is absent. The frontoparietal completely covers the epiotic eminences; the carotid canal is closed, and posteriorly exits the skull adjacent to the posterior epiotic eminence. The alary processes of the premaxillae are deflected posteriorly, at a moderate angle between 11° and 30°. The premaxillae lack long spinous medial processes. The preorbital process cannot be distinguished from the pars facialis of the maxilla, which articulates with the dorsally adjacent nasal for more than three-fourths the length of the rostrum. The pars facialis is distinctly separated from the alary process of the premaxilla, and has a narrow overlap with the dental process of the premaxilla. The quadratojugal is moderate in length. The postorbital process of the maxilla is massive, and has a broad diagonal articulation with the wide zygomatic process of the squamosal. The head of the squamosal has a wide crest; the narrow otic plate articulates marginally with the crista parotica. The dorsal and ventral parts of the stapedial footplate are about equal in size, when viewed in posterior aspect. The cultriform process of the parasphenoid narrows abruptly anterior to the optic fenestra, and has an acuminate terminus posterior to the level of the neopalatines. The sphenethmoid is ossified to the midlength of the orbit, and is not synostosed with the prootic. The neopalatines are widely separated medially, and are smooth ventrally. The pterygoid articulates with the medial surface of the zygomatic ramus of the squamosal via a long acuminate recurved process on the anterior ramus of the pterygoid. The vomers bear moderate-sized dentigerous processes located between the anterior quadrants of the choanae.

Life History

Eggs undergo direct development. Data on brooding females and embryos are as follows: LSUMZ 31971, snout–vent length 59.4 mm, containing 44 eggs each 5.5 mm in diameter, collected in June; LSUMZ 31973, snout–vent length 59.4 mm, containing 30 eggs each 9.1 mm in diameter, collected in July; and CAS-SU 5073, snout–vent length 72.7 mm, containing 69 eggs each 5.5 mm in diameter, collected in September. Parturition was induced in a female (CORBIDI 5385) having a snout–vent length 77.5 mm; she produced 59 froglets and three undeveloped ova on 17 October 2009 (Duellman and Chavéz, 2010). Her lively young had snout–vent lengths of about 11 mm. Otherwise, the smallest juvenile is USNM 345316, having a snout–vent length of 21.2 mm; it was collected in the Cosñipata Valley, Región de Cusco, Peru, on 20 June 1993.

Advertisement Call

No call has been associated with this species.

Distribution and Ecology

Gastrotheca testudinea is known from many localities, at elevations of 1100–2775 m on the eastern slopes of the Andes from Ecuador, Peru, and Bolivia; it also occurs in three isolated mountain ranges to the east of the main Andean cordillera: Volcán Sumaco and Cordillera de Cutucú in Ecuador, and Serranía de Sira in Peru (Fig. 12.61).

At night adults have been found on branches of bushes and trees in cloud forest; juveniles have been found on leaves and stems of herbs and low bushes. By day one adult was found in an arboreal bromeliad, and another was under a log.

Conservation Status

This species is designated as being of Least Concern in the IUCN Red List, even though there is a decreasing trend in populations because of habitat loss through agriculture and human settlements.

Etymology

Although Jiménez de la Espada (1871) did not state the origin of the specific epithet, it is a adjective derived from the Latin *testudo*, meaning "tortoise," and pre-

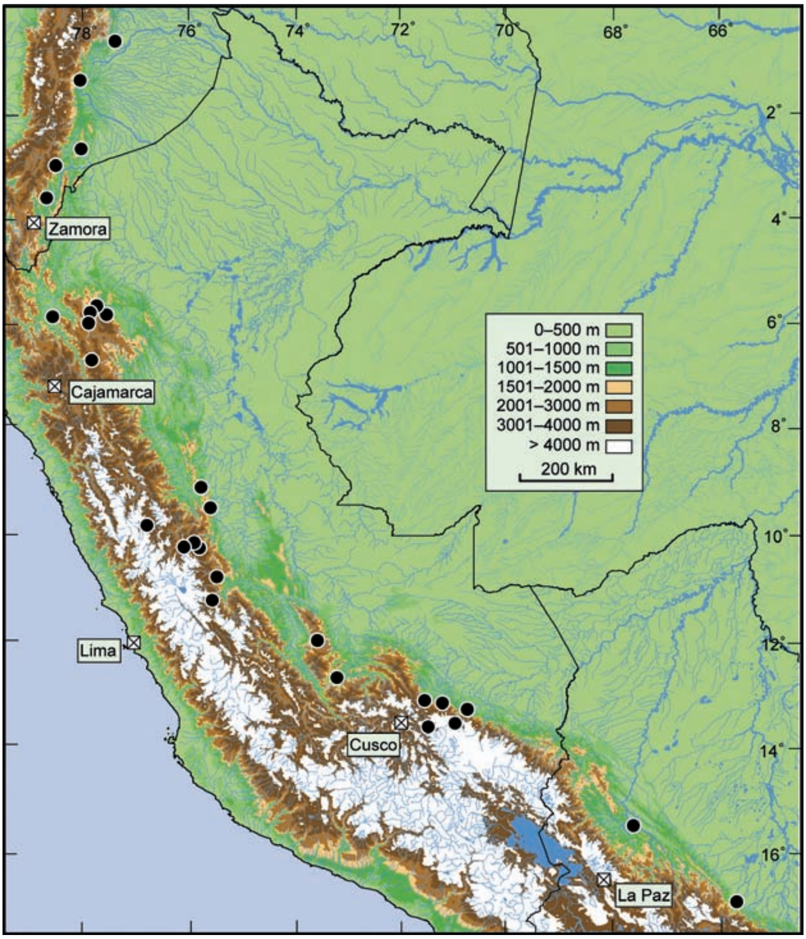

Fig. 12.61 Andean region of Ecuador, Peru, and Bolivia, showing the localities of known occurrences of *Gastrotheca testudinea*.

sumably was applied in reference to the robustness of the body.

Remarks

Duellman (1974b) provided detailed information on the holotype of *Nototrema testudineum* and the syntypes of *N. viviparum*, and noted that two Peruvian specimens similar to *Gastrotheca testudinea* presumably represented a new species and were being studied by the late Charles F. Walker. Now that I have examined many more specimens of *G. testudinea*, I believe that these two females (BMNH 81.5.13.65 from Pozuzu, Región de Huánuco, and MUSM 5 from Fundo Cinchona near Previsto, Región de Ucayali) are *G. testudinea*.

Gastrotheca (*Gastrotheca*) *zeugocystis* Duellman, Lehr, Rodríguez, and von May

Gastrotheca zeugocystis Duellman, Lehr, Rodríguez, and von May, 2004:6.—Holotype: MUSM 18675 from the Cordillera de Carpish (09°43′58.2″ S, 76°06′41.9″ W), 2910 m, Provincia de Huánuco, Región de Huánuco, Peru.

Diagnosis

This small species attains a maximum snout–vent length of 37.5 mm. The tibia length is 46.9% of the snout–vent length, and is as long as the foot. The interorbital distance is less than twice the width of the upper eyelid. The skin on the dorsum is smooth, not co-ossified with skull, and lacks transverse ridges. Supraciliary processes are absent. The heel lacks a calcar or tubercle. The tympanic annulus is smooth. The first and second fingers are equal in length; the discs on the fingers are barely wider than the digits proximal to the discs. The fingers are unwebbed; webbing is absent on the foot, except for basal webbing between the third and fourth toes. The dorsum is brown, with small irregular black marks. There are no markings on the head. A pale dorsolateral stripe is absent. The flanks are grayish brown; the venter is brown.

In most species of *Gastrotheca*, the brood pouch is single, median, and dorsal. Paired lateral pouches are known in only four species: *G. antoniiochoai*, *walkeri*, *williamsoni*, and *zeugocystis*. *G. walkeri* and *G. williamsoni*, which are species living in northern Venezuela, differ from *G. zeugocystis* in many features: larger size (70 and 54 mm in snout–vent length, respectively), tibia length more than 50% of the snout–vent length, presence of a triangular calcar on the heel and a granular interocular ridge, and fingers one-fourth (*G. walkeri*) or one-half (*G. williamsoni*) webbed. Three other species (*G. abdita*, *litonedis*, and *peruana*) are like *G. zeugocystis* in having the first and second fingers equal in length and a tibia length less than 50% of the snout–vent length; all three species differ in having much more webbing on the foot, which reaches the penultimate subarticular tubercle on the fifth toe. The tympanic annulus is granular in *G. abdita* and *G. peruana*, whereas the snout is rounded in dorsal view in *G. litonedis* and *G. peruana*. Furthermore, *G. abdita* differs by having a small tubercle of the heel; *G. litonedis* differs by having pale labial and dorsolateral stripes; and *G. peruana* differs by having a pustular dorsum, dark canthal stripe, and pale labial stripe. Superficially, *G. zeugocystis* resembles *G. ochoai*; they are alike in snout–vent length, absence of head markings, and general body pattern, but the ground color in *G. ochoai* is tan instead of brown, the first finger is shorter than the second, and the webbing on the foot is more extensive (to the penultimate subarticular tubercle on the fourth toe); furthermore, *G. ochoai* has a single median dorsal brood pouch.

Gastrotheca antoniiochoai differs from *G. zeugocystis* by having a tibia that is slightly more than 50% of the snout–vent length, compared with 46% in *G. zeugocystis*; the tibia is longer than the foot in *G. antoniiochoai*, whereas the segments are equal in length in *G. zeugocystis*. The first finger is shorter than the second in *G. antoniiochoai*, but the two fingers are equal in length in *G. zeugocystis*. The two species also differ in markings on the head: a dark brown canthal-postorbital stripe is present in *G. antoniiochoai*, whereas the stripe is absent in *G. zeugocystis*. The largest brooding female *G. antoniiochoai* has a snout–vent length of 32.5 mm, and the largest *G. zeugocystis* (a female) has a snout–vent length of 37.5 mm.

Description

The following description is based on two specimens. The body is moderately slender. The maximum known snout–vent length is 28.2 mm in a male, and 37.5 mm in a female (Fig. 12.62). The head is about as wide as long, and about as wide as the body. The snout is acuminate in dorsal view, and is rounded in profile. The canthus rostralis is straight, and is rounded in cross-section. The loreal region is shallowly concave; the lips are rounded. The top of the head is flat. The interorbital distance is about 170% of the width of the upper eyelid. The nostrils are not protuberant, and are directed laterally just below the anterior terminus of the canthus rostralis at the level of the anterior margin of the lower jaw. The diameter of the eye is much greater than its distance from the nostril. The tympanum is distinct, nearly round, and separated from the

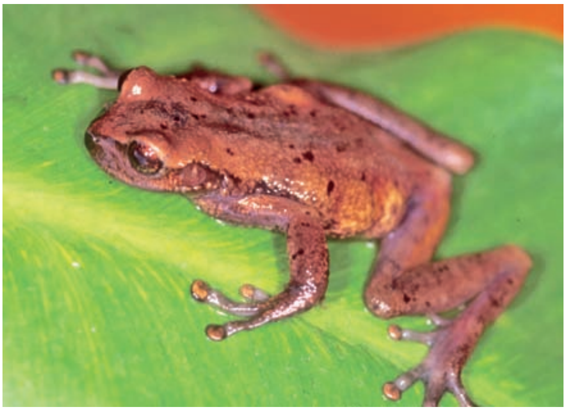

Fig. 12.62 *Gastrotheca zeugocystis* (MUSM 18675, holotype), female, 37.5 mm SVL, Cordillera de Carpish, 2920 m, Huánuco, Peru. Photo with permission granted by the photographer, E. Lehr. Copyright 2003. All rights reserved.

eye by a distance about one-half the diameter of the eye. The tympanic annulus is smooth. The supratympanic fold is rounded, covers the upper edge of the tympanum, and then curves posteroventrally to a point above the insertion of the arm.

The arm is robust, and lacks ulnar tubercles. The hand is proportionately large. The fingers are moderately long, and bear round discs; the width of the disc on the third finger is barely wider than the digit proximal to the disc. The relative lengths of the fingers are I = II < IV < III. The fingers are unwebbed, and lack lateral fringes. The subarticular tubercles are moderately large and round; none are bifid. Supernumerary tubercles are absent. The palmar tubercle is absent; the prepollical tubercle is massive and elliptical; the condition of the nuptial excrescences is unknown. The hind limb is moderately slender. The tibia length is about 47% of the snout–vent length; the foot length is about 46% of the snout–vent length. The heels lack a calcar or tubercles. Tarsal tubercles, inner and outer tarsal folds, and an outer metatarsal tubercle are absent. The inner metatarsal tubercle is small, elliptical, and not visible from above. The toes are moderately long, and bear round discs smaller than those on the fingers. The relative lengths of the toes are I < II < III < V < IV. The toes are unwebbed, except for basal webbing between the third and fourth toes; the toes lack lateral fringes. The subarticular tubercles are diffuse, and are not evident; the supernumerary tubercles are minute. and are few in number on the proximal segments of the digits.

The skin on the dorsum is smooth, not co-ossified with underlying cranial elements, and lacks transverse dermal ridges; the skin on the flanks is smooth; the skin on the throat, chest, belly, and posteroventral surfaces of the thighs is coarsely granular; the other ventral surfaces are smooth. Supraciliary processes are absent. The supratympanic fold is tubercular; there is a longitudinal row of tubercles below the tympanum; a pair of low round tubercles is present below the cloacal opening. The brood pouches are paired. The external margin of the brood pouches is U-shaped, and is elongately narrow; the opening to each pouch is under the lateral dermal fold, and extends broadly ventrolaterally to a pouch between the body wall and the skin. The dentigerous processes of the vomers are low, and are transverse at a level slightly behind the posterior margins of the small round choanae. The processes abut medially. Each process bears four teeth.

COLOR IN PRESERVATIVE

The dorsal surfaces of the head and body are brown, with small irregular black marks. The dorsal surfaces of the limbs are brown, with indistinct narrow transverse dark brown bars: two on each forearm, and three on each thigh and shank. There are irregular dark brown marks on the feet. The flanks are grayish brown, with a few scattered dark brown marks. The side of the head is dark brown; the tympanum is tan. Canthal, labial, and dorsolateral stripes are absent. The anterior surfaces of the thighs are brown; the posterior surfaces of the thighs are dull yellow; the tubercles below the cloacal opening are cream. The throat, chest, and belly are brown; the ventral surfaces of the limbs and the palmar and plantar surfaces are tan. The axilla and adjacent venter are yellowish orange.

COLOR IN LIFE

The dorsum is reddish brown, with dark brown markings; the groin and anterior surfaces of the thighs are lavender; the posterior surfaces of the thighs are orange. The venter is brown. The dorsal surfaces of the digits are bluish gray; the dorsal surfaces of the discs on the digits are orange (Fig. 12.62). The iris is reddish bronze, with black reticulations.

MEASUREMENTS

One adult female (the holotype) has the following measurements (in mm): snout–vent length 37.5, tibia length 17.6, foot length 17.3, head length 11.7, head width 11.8, interorbital distance 4.2, eyelid width 2.5, internarial distance 2.3, eye diameter 3.7, eye–nostril distance 2.8, orbit–jaw distance 1.3, nostril–jaw distance 2.0, tympanum length 2.4, thumb length 6.1, third finger length 11.0, and width of disc on third finger 1.8. One male has a snout–vent length of 28.2 mm.

CRANIAL OSTEOLOGY

The dermal roofing bones are not co-ossified with the overlying skin; the sphenethmoid is not sculptured. The nasals articulate medially; their borders are distinct from the sphenethmoid. The frontoparietals have a complete articulation medially; each frontoparietal bears a narrow supraorbital flange; an otic flange is absent. A temporal arcade is absent. The carotid canal is open. The preorbital process is not separated by a notch from the facial process of the maxilla; a postorbital process is absent. The head of the squamosal has a broad crest; the zygomatic ramus extends to the maxilla. The otic ramus of the squamosal completely articulates with and moderately overlaps the ossified crista parotica; an auxiliary dorsal ramus is absent. The parasphenoid has a short posteromedian process; the cultriform process terminates at the level of the neopalatines. The parasphenoid alae do not articulate with the pterygoids. The neopalatines are moderately separated medially, lack ventral ridges, and form the posterior margins of the choanae. The pterygoid does not articulate with the squamosal; the median ramus is not expanded medially; an auxiliary dorsal ramus is absent.

Life History

Based on the number (6) and size (6 mm) of the eggs, Duellman et al. (2004) hypothesized that eggs of *Gastrotheca zeugocystis* undergo direct development and hatch as froglets.

Advertisement Call

The call is unknown.

Distribution and Ecology

Gastrotheca zeugocystis is known only from the type locality in the Cordillera de Carpish, a north–south outlier of the Cordillera Oriental between Huánuco and Tingo María in central Peru (Fig. 12.6). The frogs were found at night on trees in cloud forest. The forest on the upper slopes of the Cordillera de Carpish is made up of low trees, with moss-covered branches. The two adults were maintained for a short while in a terrarium, where they actively climbed about on the vegetation at night and remained quiet in bromeliads or under leaves and moss by day.

Conservation Status

In the IUCN Red List, *Gastrotheca zeugocystis* is categorized as Critically Endangered, which is possibly an unrealistic designation; a more reasonable one is Data Deficient.

Etymology

According to Duellman et al. (2004), the specific name is derived from the Greek *zeugos*, meaning "pair," and the Greek *kystis*, meaning "sac"; the name refers to the paired brood pouches in this species.

Remarks

This species is known from only two specimens: the female holotype, and a male (having a snout–vent length of 28.2 mm) that was cleared and stained. In the phylogenetic analysis, *G. zeugocystis* is an outliner to other members of the subgenus and apparently is not closely related to the one other species (*G. antoniiochoai*) that has lateral pouches.

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13

In Retrospect

More than half a century has passed since my first encounter with a marsupial frog. My taxonomic conservatism in the early days of research on marsupial frogs resulted in my mistakenly considering *Gastrotheca bufona* to be a synonym of *G. weinlandii* (Duellman, 1974) and in recognizing only two species in southeastern Brazil (Duellman, 1984) when there really were five (Caramaschi and Rodrigues, 2007). The latter is a good example of inadequate knowledge of the animals. My "knowledge" of the Brazilian species was based solely on my examination of preserved specimens. Nothing substitutes for first-hand observation of the animals in their natural habitat.

During my lengthy endeavors there were moments of enlightenment and periods of frustration. For months, I had periodically examined series of specimens of *Gastrotheca "riobambae"* from throughout its range in Ecuador. Scores of specimens were spread over several trays as I sorted them by skin texture, foot webbing, and dorsal color pattern, all to no avail. One day I turned them all onto their backs, and by so doing observed distinct differences in ventral color patterns—a moment of enlightenment! I could distinguish most specimens from southern Ecuador from those in the northern part of the country. In the meantime, Linda Maxson had discovered immunological differences between northern and southern samples of *G. "riobambae"* (Scanlan et al., 1980). Obviously it was time to resolve this situation. But how? At that time, allozyme analyses based on the results of starch-gel electrophoresis were the latest form of systematic tool. In 1984, David Hillis and I collected tissues from throughout Andean Ecuador in anticipation of defining the two species; the results revealed not just two, but four species (Duellman and Hillis, 1987). At that time we thought we had resolved the systematics of the high Andean *Gastrotheca* in Ecuador. We now know that we had taken only a first step. Intensive fieldwork by Luis A. Coloma and his students has focused on the phylogeography of *Gastrotheca* in southern Ecuador; their analyses revealed three more cryptic species (Luis Coloma, in litt.).

During the many months of fieldwork, exciting discoveries were countered by the inability of finding some species. Perhaps the most frustrating event was trying to collect a taxonomically undescribed species known from a single individual from a mountain in northern Peru. Efforts to find this frog in 1979 resulted in nothing. Ten years later, four of us shivered in the cold rain and wind for two days and finally found one specimen, which we carefully photographed and preserved, with tissues extracted for DNA. Subsequently, when DNA was sequenced from many tissues of *Gastrotheca*, only one sample had degenerated, that from the single specimen of the new species (Duellman, 2013). Such were the frustrations endured for five decades.

Luckily, I began collecting tissues in the early 1970s for Linda Maxson to use in immunological studies. Usually tissues were removed from only one individual of a species. Her large collection of tissues has been maintained under the care of Blair Hedges at the Pennsylvania State University. Nearly half of the species in the phylogenetic tree in chapter 3 are represented by tissues that I collected. Many of them (e.g., *G. ovifera*, *walkeri*, *weinlandii*) are the only known tissues of those species, some of which may now be extinct.

Genomics is the contemporary "bandwagon" in evolutionary biology, and this is especially evident in systematic biology. Time and time again, genes are said to provide the truth about evolutionary relationships. Perhaps, but biologists need to realize that we are witnessing the adolescent stage of molecular systematics, as evidenced by a continuous reinvention of the wheel—how to analyze the genomic data. A phylogenetic arrangement based on only four of a dozen or more known morphological characters would never be accepted for publication. Yet a phylogeny based on four genes (as I have done here) is acceptable. Taxon sampling in many genomic studies has been remarkably small. Frost et al. (2006) analyzed genomic material from 522 species of amphibians that provided an excellent foundation for future studies. In the second part of this lengthy publication, the authors proposed a new classification; much of this taxonomic exercise was based on extremely poor taxon sampling. For example, using molecular data on only 16 of more than 800 species of direct-developing frogs that were later placed in the unranked taxon Terrarana by Hedges et al. (2008) had resulted in Frost et al. (2006) proposing a completely illogical classification. Poor taxon sampling and limited genomic data by these authors also resulted in their placing the six taxa of marsupial frogs and their allies in three families! Nonetheless, taxonomic and nomenclatural changes can actually initiate progress in understanding the systematics of some groups by accelerating more thorough research.

The deposition of sequences in GenBank provides the scientific community with access to genomic data on more and more species. Yet one must be aware of possible misidentifications and changes in nomenclature. Perhaps the most distressing aspect of GenBank is that it gives unscrupulous investigators the opportunity to mine other scientists' hard-gotten data for their own analyses, which the former group of individuals publish and on which classifications are based, without these investigators gathering any data of their own (e.g., Pyron and Wiens, 2011).

In recalling the last half century, I wonder how much I have missed in the field. Some memorable things have been brought to my attention by cherished colleagues (Fig. 13.1). Not all may be so humorous, and some may be significant. Maybe some of these, as well as others thus far never conceived, will be discovered by my followers. In finishing this opus, I am reminded by a series of poems, and so apologize to Mason Williams and his *Them Poems* (Vee Jay Records, 1964).

Them Marsupial Frogs
How about them Marsupial Frogs,
Ain't they sumpin'?
Totin' them youngins on they back.
Some leave taddies and
Some, itty-bitty frogs
Out in the tree tops or
Down in the bogs.
Look at them Marsupial Frogs.
Ain't they neat?
Pushing them big eggs
With they hind feet.

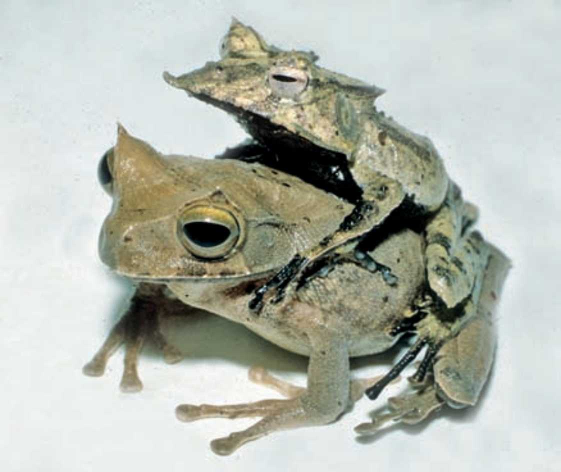

Fig. 13.1 An illicit relationship featuring a male *Hemiphractus fasciatus* and a female *Gastrotheca cornuta* (not posed). Photo by C. W. Myers, KUDA.

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About the Author

William E. Duellman's first encounter with a marsupial frog was in July 1963 in the montane rainforest in eastern Darién, Panama. This discovery would eventually lead to studies throughout much of South America—the Gran Savana and Sierra de la Costa in Venezuela to the cloud forests on the slopes of the Andes and the páramo and puna above those forests in Colombia, Ecuador, Peru, and Bolivia, with an extension to the Andes of Argentina. During this fieldwork he encountered hundreds of specimens of marsupial frogs. Each specimen was carefully examined, as were those held in museum collections in Europe, North America, and South America. Over time his studies resulted in numerous scientific papers and finally this book, which is a synthesis of half a century of research.

Most of Duellman's academic life has been at the University of Kansas, where he was a professor in the Department of Systematics and Ecology and Curator of Herpetology in the Natural History Museum (now Biodiversity Institute) and now serves as Professor and Curator Emeritus. He has published more than three hundred scientific papers and has authored or edited nine other books. Among these book are *Hylid Frogs of Middle America*; *Biology of Amphibians* (with Linda Trueb); *Cusco Amazónico: Lives of Amphibians and Reptiles in a Tropical Rainforest*; and *Terrestrial-Breeding Frogs* (*Strabomantidae*) *in Peru* (with Edgar Lehr). Duellman continues to be an active researcher and writer. The photos show Dr. Duellman in 1963 and in 2013.